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BIRD NAVIGATION

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PREFACE

The presumed navigational powers of animals, and in particular those of birds, have attracted scientific attention for more than a century. It is during the last ten years that a fresh impetus has been given by the advancement of new theories and the development of new experimental techniques. This monograph attempts to survey the present position which, perhaps momentarily, appears to have some coherence. The path of progress in this field is littered with discarded theories and it is possible that the one at present favoured may be found inadequate. But both the existence and the physical bases of bird navigation are now firmly established, and it is more likely that future developments will lie in a better appreciation of the way in which a bird interprets and acts upon the information available to it.

I should like to acknowledge my debt to those who both encouraged and enabled me to undertake research in this field, particularly Professor Sir James Gray, F.R.S., and Dr W. H. Thorpe, F.R.S., and to those bodies which provided financial backing, the Department of Scientific and Industrial Research and the Royal Society. I am most grateful to Dr George Salt for his help and advice in the preparation of the monograph.

G. V. T. M.

3 November 1954

CHAPTER I

The Contributions of Taxonomy and Field Observations

THE scope of this short book is limited to the study of only one aspect of bird migration, that of the manner in which birds find their way in unknown country; their navigation. Further, the bulk of the book will be concerned with only one type of approach, the experimental. It will soon be obvious that the experiments are very crude compared with those elegant exercises that require cathode-ray tubes, micro-pipettes and the like. But in studies of animal behaviour, even simple experimental interference is not justified until the normal activities have been studied in detail, and problems have been raised and theories produced that only direct experiment can solve or test. We are fortunate that the study of bird migration has a firm, expanding basis of the essential taxonomic data and field observations. These have been accumulated not only by professional zoologists, but by the efforts of spare-time enthusiasts.

Field observation and the systematic collection of specimens have allowed the migrations undertaken by the different species to be mapped in outline. Often simple specific identification is sufficient to establish that remarkable migrations are taking place. This is the case where the species has a limited breeding area. Thus the Bristle-thighed Curlew[1] nests only in a coastal strip of Alaska but winters in Tahiti, Hawaii and other Pacific islands up to 6000 miles away, with minimal sea-crossings of 2000 miles. Unlike the more often quoted Golden Plover, this species is found only on those islands and not on the coasts of Asia and America as well. Even so the wintering area covers an arc of 45° from the breeding quarters and we cannot assert that any individual Curlew is flying to a particular pin-point of land, but only that the migration must at least have a strongly directional trend. The return journey from these scattered islands to the restricted breeding grounds involves the greater navigational feat, though even this is less startling than that of the Great Shearwater. These birds range over the whole of the Atlantic Oceans, penetrating to 60° N. Yet to breed they must return in their millions to the tiny Tristan da Cunha group of islands lying 40° S., spread over only 30 miles of ocean and lying 1500 miles from the nearest land mass.

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[1] Throughout this book the accepted English names of birds have been used in the belief that they will convey more to the non-ornithologist (and perhaps to the majority of ornithologists) than the Latin ones. The addition of the latter on each occasion is tiresome to the reader, so a complete list of the Latin equivalents of English names used is given on p. 121.

Where the species has a wide breeding range, the often maligned 'splitter' among the taxonomists is of great assistance. If the birds can be divided into sub-species and geographical races on the basis of minute differences in body form, the movements of birds from a particular area can be followed in more detail. The results show a strong tendency for a local breeding population to reassemble in quite localized wintering areas. The six sub-species of the Fox Sparrow which breed successively down the west coast of North America are found wintering in the *reverse* order, i.e. those breeding farthest to the north winter the farthest to the south. There are many other examples of migrants covering greater distances than they 'need', such as the Great Skua in Japan which is assigned to the race breeding round the Antarctic continent and not to the much nearer New Zealand race.

Taxonomic studies also established that in many species, such as Starlings, the young birds of the year make their migration quite independently of the adult birds. In such cases there can be no question of the latter acting as guides. The extreme of juvenile independence is of course provided by the Cuckoos, which nevertheless perform remarkable migrations. The Bronze Cuckoo, reared by non-migratory foster parents in New Zealand, migrates to the Solomon and Bismarck Islands lying 2500 miles N.N.W. over the open sea. There are two isolated islands on the track and some birds pass via eastern Australia, but minimal sea passages of 900 miles are necessitated by this route.

The acme of methods for labelling migrants according to their place of origin is that of ringing (or banding as it is more accurately known in America). Aluminium rings (bands) are placed on the bird's leg either when it is a nestling or when it has been trapped as an adult. The ring bears a code of letters and numbers which is unique to that class of ring issued by a particular organization. The latter's name and address is also included on the ring. The method has been widely adopted in the last half-century and its use has reached considerable dimensions. The total number of birds ringed is not known, but it exceeds ten million for Germany, Great Britain and North America alone. Subsequent reports of birds that have been ringed range from about 20 % in species shot for sport or as vermin, to a fraction of 1 % in the smaller passerines and in pelagic species. Allowance must be made for some bias in the proportion and location of such recoveries. They will reflect to some extent the distribution of the human population, and in particular of that portion of it that is literate and will report such finds, rather than use them as charms. Again in most species the bulk of the information will relate to young birds in their first year, owing to their greater mortality. Despite such imperfections in the method, results of the highest importance have been obtained.

On the one hand some of the most exaggerated migrations have been confirmed, such as that of the Arctic Tern. These birds have been shown to migrate from the Canadian Arctic, where they nest within 10° of the North Pole, to the Antarctic pack-ice via the west coast of Africa. The double journey is equivalent to circling the earth at the equator. On the other hand, it has been established that, after long journeys, migrants return to breed, year after year, in the same nest site. For some species the much more difficult achievement of identifying the same individual repeatedly *wintering* in a small area has been reported (e.g. Tettenborn, 1943). On a more general level the re-forming of localized breeding populations in localized wintering areas has been amply confirmed. Indeed the typical migration has come to have the appearance of a 'shuttle' service between two small areas. This would require as a bare minimum of navigational equipment the ability to fly an accurate bearing-

and-distance course. In many cases, that of the Great Shearwater for instance, a more precise form of navigation would seem to be needed.

The technique of direct observation has been applied with great success to the study of migration in progress—'visible migration'. A considerable body of data has been accumulated particularly in Holland, but more recently in Sweden and the United Kingdom. Many of these data are rather indigestible and Thomson (1953) has rendered a valuable service by writing a summary of the main conclusions that have been reached. His paper serves as an introduction to six others describing the work which has been carried out in different countries, all in the same issue of *Ibis*. Simple observation of the migrants in flight lacks the precision of knowledge as to their origins and destinations inherent in the methods based on taxonomy and ringing, but it has added much useful information concerning orientation.

For many years there was great controversy as to the method of migration. There were those, following Middendorf (1855), who believed that migration took place in one general direction, on a broad front. Opposing them were the followers of Palmen (1876) who insisted that the migrants passed along certain restricted routes, on a narrow front. As is so often the case in biological controversy the correct answer is a compromise. Geyr von Schweppenburg (1922, 1929, 1948) formulated such a theory. He suggested that there was indeed a directional trend to migration, the birds flying in a 'standard direction', typical of their particular population, while over uniform terrain or the sea. But in addition there were 'leading-lines' formed by the boundaries between favourable and unfavourable terrain, between land and sea, hill and plain, forest and savannah, desert and fruitful land. When the birds encounter such a leading-line they tend to fly along it, forming a narrow and concentrated stream just as if they were passing along one of Palmen's 'routes'. But when the obstacle is passed, or the urge to fly in the standard direction becomes paramount, the stream widens out into the broad front again. Field work done in Holland, particularly by L. Tinbergen and by van Dobben (summarized by van Dobben, 1953), has amply vindicated this conception.

It has been demonstrated that birds are more easily deflected and concentrated when flying low—as they do for instance on encountering a headwind (Fig. 1). Visible migration then becomes much more obvious and this has led to the quite unjustified conclusion that the migrants prefer such conditions. The evidence is that migration can occur with wind from any direction and that the effects of wind, though important, are incidental. Head winds cause deflexions by increasing the effect of (mis)leading-lines, while beam winds impose sideways drift. Drift can be, and apparently is, corrected over land by reference to topographical features. Over the sea it may go completely unchecked, particularly at night. Williamson (1952) has stressed the importance of this factor and it would seem that most of the night migrants arriving on the east coasts of the United Kingdom are unintentional visitors. Williamson's additional hypothesis that the wind-drifted migrants actually fly downwind is based on rather slender evidence. Vleugel (e.g. 1952, 1953) considers that wind direction has an important, though secondary, guiding function.

The standard directions of a number of passerine species have been determined with some degree of certainty by observation in open country, and the general trend, N.E.–S.W., deduced from taxonomic and ringing work, has been confirmed. There are variations according to the areas of origin. Starlings passing through Holland and deriving from the Baltic States, fly mainly between W.S.W. and S.W. Those passing through Switzerland and deriving from central Germany fly between S.W. and S.S.W. There are suggestions that some species, e.g. Skylarks, have two standard directions that come into predominance at successive stages of the migration.

The bulk of these observational data is limited to a few passerine species, and to their autumn passage, when there is a preponderance of young birds. The conclusions derived from them and in particular the implication that bearing-and-distance navigation would suffice, should therefore be treated with caution. Also a great deal of migration occurs at night. The evidence suggests that spring migration by day is a much more urgent process, and leading lines have little influence. Until recently information on night migration was very scanty.

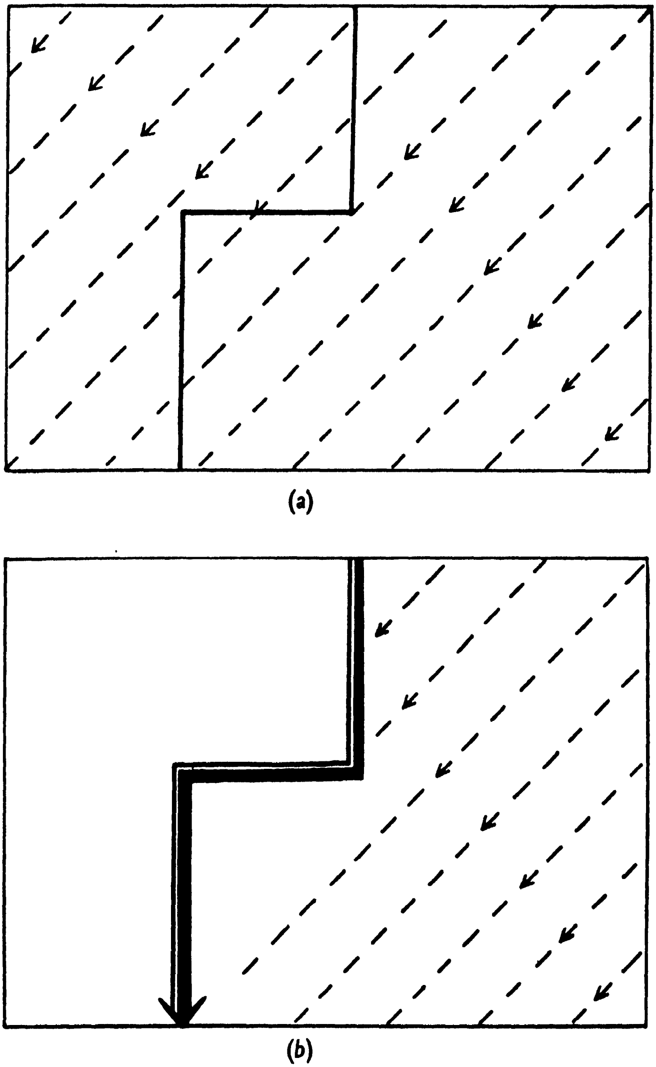


Fig. 1. Broad and narrow front migration. (*a*) At night, and by day when birds are flying high with a following wind, movement in the 'standard' direction continues without reference to topographical features such as the border between two types of terrain. (*b*) By day when birds are flying low with a head wind, the border becomes a 'leading line', and the advance becomes canalized into a narrow stream following its directional trends.

The clearly abnormal behaviour at lighthouses was of little help, and the birds' movements could only be inferred from flight-calls and the variation in the numbers of such birds present during the day. Recently, Lowery (1951) has used the ingenious, if laborious, method of observing the passage of birds across the moon's disk. This provides a cone of observation sweeping slowly across the sky. Elaborate calculations are needed to ascertain the effective size of this cone, but these have been reduced to tabular form. The method is, of course, limited to clear moonlit nights when only a part of nocturnal migration occurs, and identification of the birds is extremely rough, so that only a general picture of migration as a whole can be built up. Nevertheless, interesting results have been achieved by a network of observers in America. Most important is the conclusion that nocturnal migration is of the directional, broad-front type with little evidence of concentration along leading lines.

CHAPTER 2

The Experimental Evidence for Bearing-and-Distance Navigation

IN those species where the young migrate independently of the old we have a natural experiment showing that any tendency to fly in one direction must be part of the bird's innate behaviour. It was possible that where young and old migrate together the former would have to *learn* the migration direction. To test this, young birds were held back in the area of their breeding until all others of their species had departed. In the first migration period 247 White Storks treated thus (Schüz, 1949) gave sixteen reports. All were between S.S.E. and S.W., in the normal direction but rather more scattered than usual. Fifty-four Prairie Crows gave 'some 60 %' recoveries of which 'not a single bird had deviated significantly from the standard fall direction' (Rowan, 1946).

A test better designed to show that the inherited tendency was to fly in a direction without relation to local topography was to transport eggs or nestlings to some completely foreign area. The birds were reared there and released when all local migrants had passed through. Taken from East Prussia, reared and released in western Germany, 144 White Storks gave a number of reports based on ringing recoveries or observations of these plumage-marked birds (Schüz, 1949). Their tracks can be mapped with some precision (Fig. 2) and show a strong tendency to lead S.S.E. This is the appropriate direction for the population from which they were drawn, but quite distinct from that (S.W.) for the species in the area of their release. A rather similar result was obtained with twenty White Storks released in Frankfurt, though these soon encountered high mountains and were deflected to the S.W. The Essen birds likewise showed scattering when they reached the Alps. Rowan (1946) trans-

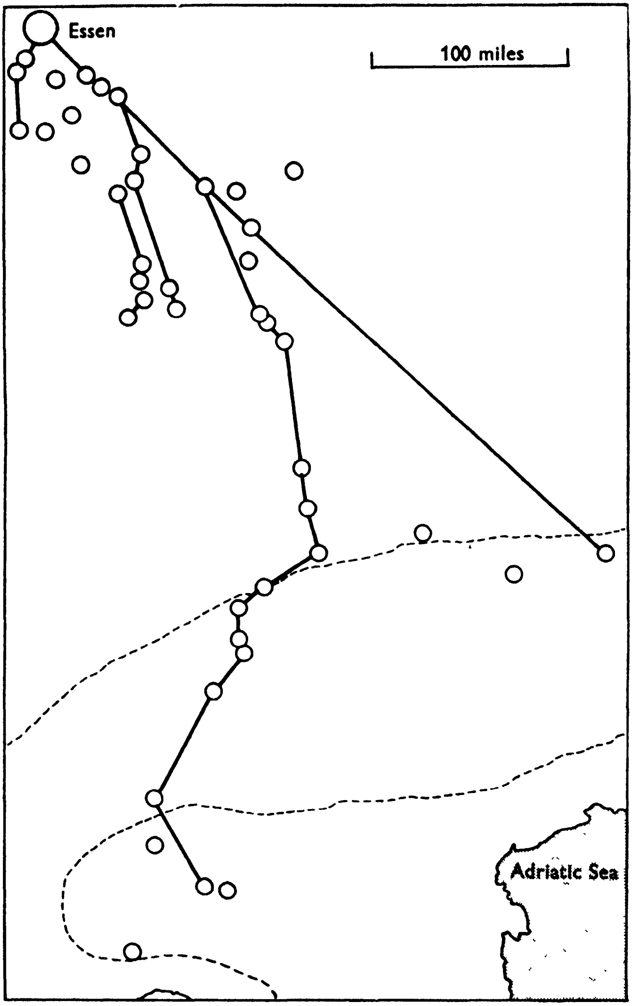


Fig. 2. Migration of young East Prussian Storks reared and released in West Germany in the autumn after all old birds had departed. Reports probably referring to the same party of birds are linked together. The dotted lines enclose the Alps. Note the S.S.E. trend. (After Schüz, 1949.)

ported eighty Prairie Crows from Alberta to Manitoba, Canada, but obtained only three returns, adhering to the S.E. direction typical of the Alberta population.

An even more stringent test was to rear and release the young birds in areas where their species do not breed at all. Twenty-one White Storks from East Prussia were reared in England (Schüz, 1938*b*). They moved away at the usual time and spent several weeks flying up and down the south coast, apparently loath to cross the Channel. It is assumed that they eventually did continue their southward migration for they disappeared, and two were promptly shot on the French side. Thirty-six Shelduck reared at Sempach in Switzerland from eggs laid at Sylt in north-west Germany (Schifferli, 1933, 1935) gave inconclusive results. Nearly half remained at Sempach over the first winter and another fifteen were recovered short distances away. Four were recovered at distances of 140–370 miles, all between north and west. This *might* be interpreted as an attempt to regain their original area, but is more likely a debouchment from the mountains by these typically shore and estuarine birds. The Sylt population migrates south-west. A pair of the experimental birds returned to Sempach for several years and may have bred there (Schifferli, 1943*b*). McCabe (1947) reared 192 Wood Duck 200 miles from the point where they were laid. Next spring nine or ten pairs returned to their foster home and bred. A careful check at the 'ancestral' home failed to reveal any of the experimental birds. Schüz (1938*a*) substituted Common Gull eggs from the Hiddensee for Black-headed Gull eggs at Rossitten, 310 miles eastwards. From seventy-nine fledglings ringed, five returned to Rossitten and a pair bred. Similarly some of the Common Gulls taken as young from the Baltic coast inland to Silesia by Stadie (1938) returned to breed there in later years (Krampitz, 1941). While the Wood Duck and Common Gulls provided no information on their migration direction, they did show a strong tendency to return to their foster homes.

Inherited directional tendencies are readily modified by the example of older birds of the species. This was shown when 754 White Storks from East Prussia were released in West Germany while Stork migration through the area was still in progress

(Schüz, 1950). The recoveries, shown in Fig. 3, have a strong tendency to the south-west, approximating to the direction taken by the 'foreign' Storks and contrary to that prevalent in the homeland (compare Fig. 2). Similar results appear to have been achieved by Williams & Kalmbach (1943) with 131 Canada Geese and 213 duck of various species. For the storks, geese and ducks, recoveries subsequent to the first migration, though few in number indicate a return to the area of the foster home for breeding. Packard (1947) reports a similar return for several years, of a hand-reared American Robin which had been transported 70 miles as a nestling. Migration can even be induced in non-migratory stock by the example of older, migratory individuals of the same species. Thus Valinkangas (1933) and Pützig (1938) hatched eggs obtained from English, non-

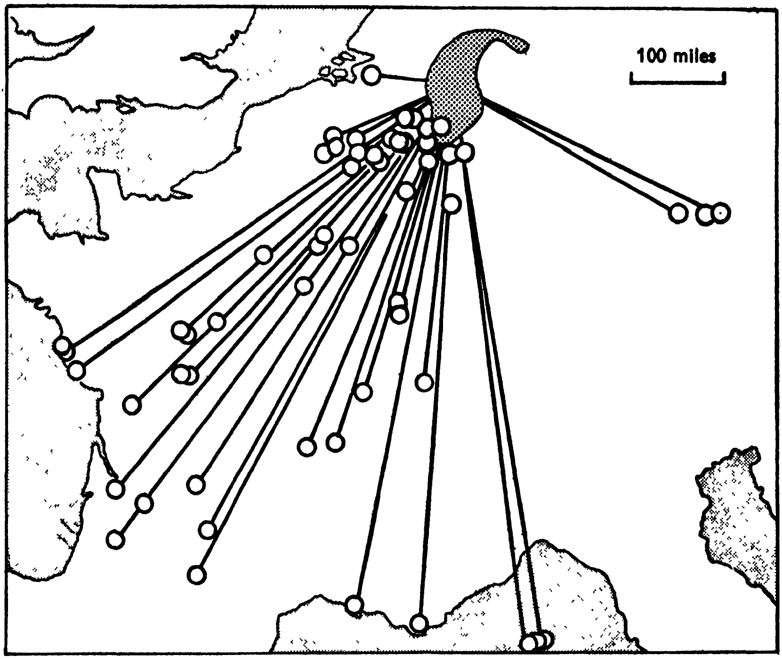


Fig. 3. Migration of young East Prussian Storks reared and released in West Germany in the autumn while old birds were migrating. Area of releases shaded. Note S.W. trend. (After Schüz, 1950.)

migratory Mallard in Finland and East Prussia. The 116 young which were reared were allowed their freedom with the local, migratory Mallard and eventually departed with them. Nineteen recoveries were made up to distances of 1500 miles, all within the normal winter ranges of the local populations. Of eight birds restrained in East Prussia until the local migrants had left, five remained over the winter and bred there. Of the experimental birds that migrated from their foster home in Finland more than half returned there to breed. The reverse experiment, rearing migratory stock among local non-migratory stock of the same species has not been reported. However, only six out of ninety-seven of McCabe's Wood Ducks released among a flock of a hundred semi-tame Mallard remained with them over the winter.

Large-scale transplantation experiments such as those described above require extensive rearing facilities. Another method has therefore been to capture young migrants that are actually in passage in the autumn and transport them considerable distances to one side of the migration axis, outside the area normally reached by birds passing through the point of capture (determined by ringing recoveries). Species easy to trap in large numbers, and preferably those liable to be shot subsequently have been favoured. This is because their subsequent movements have been largely pieced together from their ringing recoveries, although plumage marking has been used. Table 1 lists the four large-scale experiments that have been reported.

Table 1. *Displacement experiments with autumn migrants*

Species	From	To	Total	Recovered	Author
Starling	Memel	Breslau Dresden	3013	95	Kratzig & Schüz (1936)
Starling	Texel	Geneva Basle Zürich	*c.* 5500	150	Perdeck (1953)
Sparrow Hawk	Heligoland	Gimmel (Silesia)	209	36	Drost (1938)
Hooded Crow	Rossitten	Berlin	232	54	Rüppell & Schüz (1948)

In all these cases the same general conclusion was reached. The young birds continued to migrate from the release point in that direction which their congeners follow from the trapping point. The transported birds thus followed a course roughly parallel to the normal and wintered in areas far outside the usual range. Fig. 4 shows in diagrammatic form the results obtained by Perdeck (1953). Although recoveries in the following spring and in subsequent seasons were naturally much fewer, it has generally been found that the experimental displacement was maintained. The young birds took up breeding quarters outside the normal range and returned to the 'new' winter quarters. We have already seen that young birds readily adopt a foster home. This further result indicates that the summer home likewise is not fixed even when the birds have been reared there. Confirmation was obtained in experiments involving the translocation of *spring* passage migrants. Drost (1934) moved ninety Starlings and nine Ring Ousels from Heligoland to Gimmel, but obtained only two recoveries. Rüppell (1944) moved 625 Hooded Crows from Rossitten to Flensburg and Essen, obtaining 121 recoveries. Again the young birds showed a parallel displacement, breeding outside the normal range and maintaining the displacement in subsequent years.

These displacement experiments with passage migrants required very considerable excursions into 'logistics'. It is therefore most unfortunate that their results cannot be taken as *conclusive* proof of the existence of an innate directional tendency in the experimental birds. This is because, for the whole area involved, the general tendency is for migration to be on a N.E./S.W. axis. We have already seen how easily the migration of young birds is influenced by the example of others. There was thus a strong possibility that the translocated birds simply joined up with passage migrants at the release point and proceeded with them to their winter quarters. It can be argued that the recoveries of the young Starlings shown in Fig. 4 approximate more closely to the Dutch (W.S.W.–S.W.) than to the Swiss (S.W.–S.S.W.) pattern, but many more recoveries would be required for this to be convincing. However, Rüppell (1944) carried out the critical test of releasing birds in an area where local migration had ceased. This was possible on spring

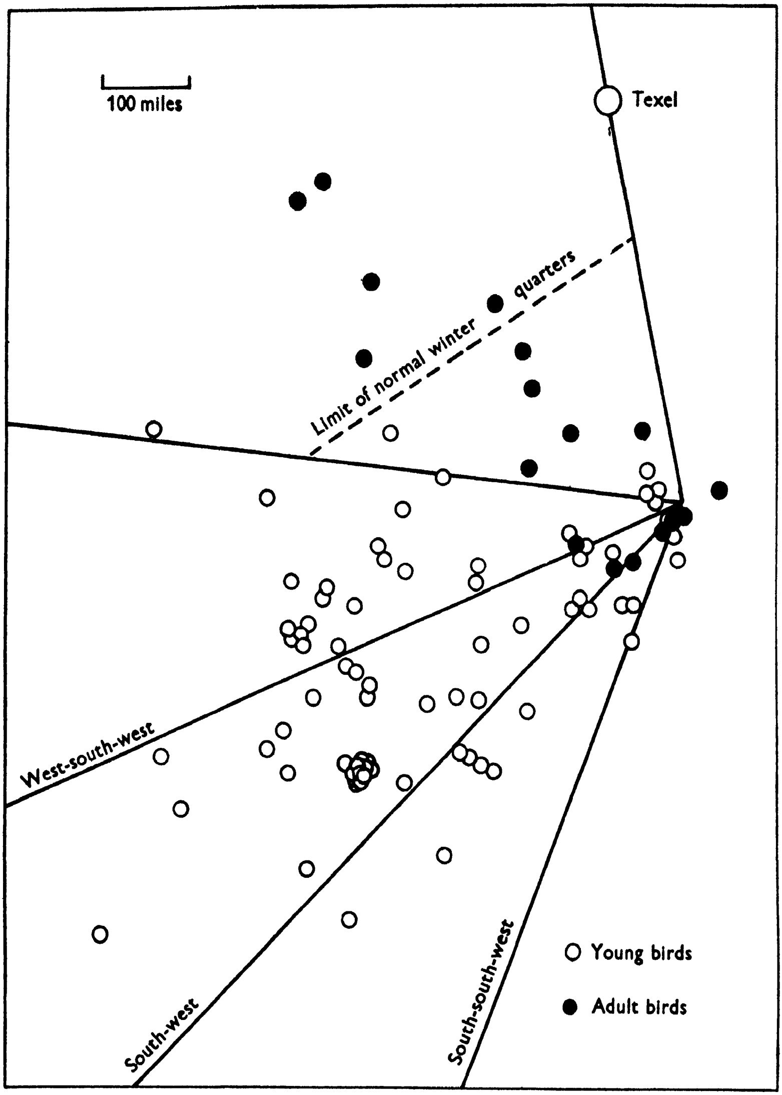


Fig. 4. Recoveries in the following winter of Starlings caught on autumn passage through Holland and released in Switzerland. Results for three release points coincided. Note young birds maintained the normal *direction* (W.S.W.–S.W.) but that old birds altered direction to regain the normal winter quarters. (After Perdeck, 1953.)

migration which is much less prolonged than the autumn passage. During this experiment 271 Hooded Crows were moved from Rossitten to Frankfurt (630 miles). The subsequent recoveries gave a rather wider scatter than in Rüppell's other experiments, but the tendency was strongly in the north-eastern sector (Fig. 5).

Finally, Kramer (1949, 1950*a*) was able to show that directional tendencies were manifest in caged migrants, Red-backed Shrikes, Blackcaps and Starlings. It had long been known that such birds when caged show periods of intense activity, and that these coincide with the times at which migration of the species is taking place. This phenomenon of *Zugunruhe* has been used in studies of the physiology of the migration impulse (Palmgren, 1949, for summary). By careful study of the movements of the captive birds, Kramer was able to show that they had a strong directional component; that the birds tended to head in a certain direction whether they were hopping about or sitting and beating their wings. Although some anomalous tendencies were found, as a general rule the direction taken up by the caged bird corresponded to that in which it would be flying on migration. The direction was maintained when landmarks were excluded and the cage erected in different places. This method of studying the problem under laboratory conditions has not only confirmed the existence of innate directional tendencies, but has facilitated investigation of the sensory clues by which the direction is determined. This is discussed in Chapter 5.

A purist may object to the assumption that directional tendencies are innate, on the grounds that no experiment has yet been reported in which young birds reared by hand from the egg showed such tendencies. It would be pleasant to have this final check, but a 'reasonable man' would not insist on it, since it is hardly likely that nestlings could learn the required direction from their parents while still in the nest.

Another feature of migration displacement experiments is that not only is the original direction maintained but the area of recoveries extends, roughly, for the same *distance* from the release point as it would for unmolested birds passing through the trapping point. This cannot be attributed to the example of local fellow-travellers in Rüppell's Frankfurt experiment

(Fig. 5). The young birds finally halt in areas considerably different ecologically from those in which their flight would normally terminate. The implication is that the length of the migration journey is controlled by internal factors, that migra-

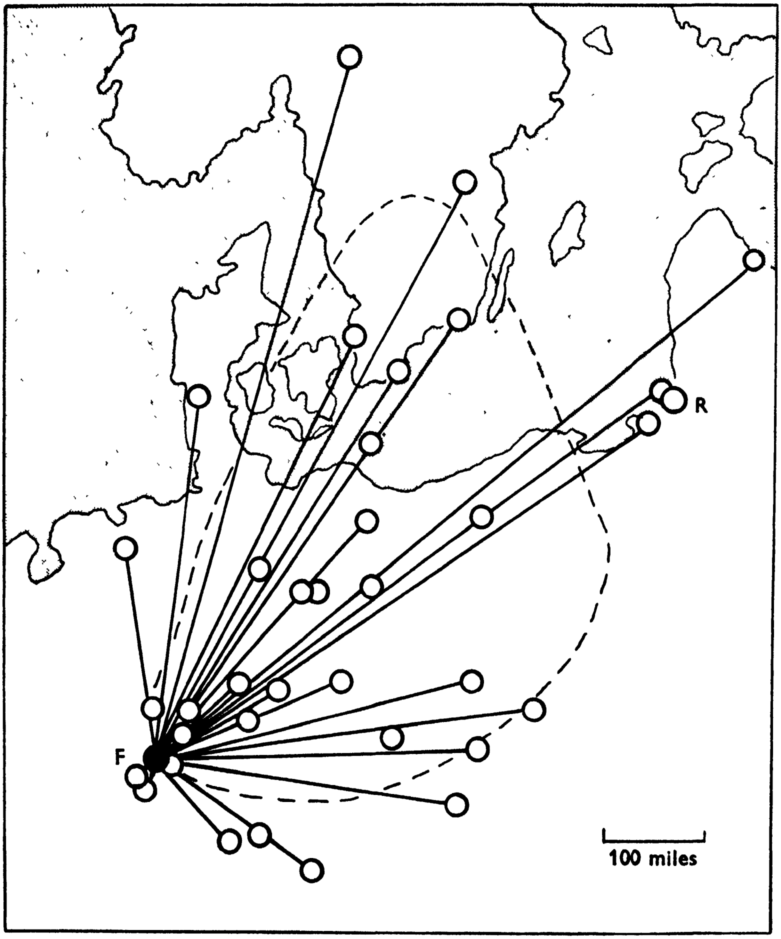


Fig. 5. Recoveries in following summers of young Hooded Crows caught on spring passage near Rossitten (R) and released at Frankfurt (F) after local migration there had ceased. The dotted line encloses an area equivalent to that in which the birds would normally be found had they continued their flight from Rossitten. Note N.E. trend and normal distance of migration are maintained. (After Rüppell, 1944.)

tion continues only while the 'drive' is present. That the migration impulse is relatively short-lived is amply confirmed by studies of caged migrants. It is outside the scope of this monograph to discuss the great amount of work that has been done on this problem, and on the various external changes, notably day-length, which act as pace-makers. Useful summaries have been given by Rowan (1938) and Farner (1950). The requirement that migration, once started, should proceed at a fairly steady rate is also confirmed by experimental and observational studies (see also Chapter 4, p. 38).

The young bird is thus innately equipped to carry out the simple procedure of a bearing-and-distance flight to a hitherto unknown area. Provided no unusual circumstances are encountered this enables the untutored population to shuttle back and forth between summer and winter homes. Indeed, it might be considered that this would suffice to carry a bird through all its subsequent migrations. The end-point of the migration would become a little more precisely defined as the bird became familiar with the topography of its two homes. But in fact the displacement of older birds, with experience of at least one return migration and one season's breeding in the summer home, produced very different results from that of the young birds which we have been considering. There was a strong tendency for the recoveries of these older birds to lie in the direction of, or actually within, the normal winter and summer areas. They ignored the 'standard direction' and the example of local passage migrants at the release point. The difference between young and old birds is best shown in Perdeck's work with Starlings (Fig. 4) since the proportions transported, and hence recovered, were more nearly equal (3·5 young : 2 old) than in the other studies. But tendencies to return to their normal areas were shown by the older Sparrow Hawks and Hooded Crows. McIlhenny (1934, 1940) reports similar results with Mallard, Pintail and Teal which in the United States have three main 'fly-ways', the Atlantic and Pacific coasts and the Mississippi valley. In this experiment 440 of these duck were taken from the Mississippi valley and released on the coasts. There were ninety recoveries of which seventy-nine had returned to the Mississippi fly-way.

These older birds, instead of passively accepting the experimental displacement, were in fact actively *homing* to a previously known area. This would pose very much more considerable navigational problems. The ways in which these are solved cannot be studied in detail by the displacement of passage migrants since, amongst other things, it will be necessary to know the precise area to which the bird is striving to return, and to maintain watch there to see if and when the return is effected. Some species do habitually make long foraging flights from the nesting area, but it will also be necessary to ensure that the bird is able to home from a previously unknown area. It is therefore necessary to force the birds to undertake long flights back to their home by removing them artificially and releasing them at a distance.

Recently, Griffin & Goldsmith (1955) have reported another form of one-direction navigation. Common Terns breeding on the east coast of the U.S.A. headed consistently in a south-easterly direction when released inland. This was so when home lay to the S.E., E.N.E., N.E. or S.S.W. and was independent of wind direction. Release points such that home lies in a radically different quarter are needed to confirm that we are not dealing with a crude form of homeward orientation (Chapter 4). But it appears probable that we have here a directional tendency which serves to bring these particular birds back to the coast, and quite distinct from their migration direction, N.E./S.W.

This and other footnotes at the end of chapters refer briefly to papers received between submission of the typescript and final proof correction, 14 March 1955.

CHAPTER 3

Homing Experiments: Their Technique, Results and a Possible Simple Explanation

HOMING experiments have a respectable antiquity. Indeed one of the oldest inscribed records, Sumerian tablets of perhaps 5000 years ago, sets out the Gilgamesh epic with its reference to a version of the Flood legend and the homing behaviour of dove, Swallow and Raven. Pigeons were certainly used to convey messages by the ancient Egyptians, the Greeks (Ovid) and Romans (Pliny) and generally throughout the Middle East. It was not until the nineteenth century, however, that the advent of railways enabled full use of the potentialities of Pigeons to be made. The practice of racing Pigeons for sport began in Belgium about 1825, and it is clear that the intensely selective breeding which has occurred over the intervening years has greatly improved the stock. The sport has spread to all parts of the world, and in Great Britain alone more than a million birds are maintained for this purpose. During the recent war more than 200,000 British birds were used for all manner of communications. General accounts of pigeon-racing techniques have been given by Tegetmeir (1871), La Perre de Roo (1872), Thauziés (1898), Dusolier (1903), Riviere (1923), Rochon-Duvigneaud & Maurain (1923), Most (1926), Knierim (1943) and Nichol (1945), and there is a vast popular literature.

For a long time it has been known that the swiftest and surest returns were obtained with Pigeons carefully trained by releases at gradually increasing distances in *one general direction.* The practice was centuries old when described by Moore (1735). In pigeon-racing the overriding aim is a return in the shortest possible time, and, such is the competition, a few seconds at the end of a flight of many hours often make all the difference. As a result pigeon-fanciers have adhered strictly to a single line of releases, the race liberation points being as nearly on that line as railway facilities permit. Thus fanciers around Cambridge have release points at Peterborough, Grantham, Newark, Retford, Doncaster, Selby, Northallerton, Durham, Morpeth, Berwick, Arbroath, Thurso and Lerwick (550 miles). Long sea-crossings form serious obstacles and impose limits in the case of British birds. In America, however, races of up to a thousand miles are regular features.

While a result of this one-direction training could be the building up of a corridor of well-known country and a chain of visual landmarks, the later stages involve release at distances of a hundred miles or more from the previous point, precluding a direct view of the latter. Under race conditions (Dinnendahl & Kramer, 1950) the picture is often obscured by more experienced birds being released with the newcomers. But it seemed fairly clear that the pigeons in fact learnt to fly in that particular direction on release. This was confirmed by Schneider (1906), Kramer & St Paul (1950*b*), Matthews (1951*b*) and Riper & Kalmbach (1952). These workers showed that after such directional training, pigeons released in an entirely new direction still flew in the accustomed direction though this no longer took them towards home. Hitchcock (1952) was able to follow such misguided flights from the air. We thus have a direct analogy with the one-direction flight tendencies of young migrants, though in the present case the direction is learnt and is *not* innate. Pigeons can be trained in any direction that is convenient. Again, like the wild birds, Pigeons home only to the place where they were raised and not to that from which their stock originated, and 'home' does not appear to become a permanent feature for them until they themselves have bred there. Up to that time they can fairly easily be settled in a new home, but thereafter this becomes extremely difficult.

For a time the emphasis on one-direction flights resulted in a general belief that the learning and detection of such a direction was the limit of navigational ability in Pigeons, and that without it any homing could be attributed to a general search for known visual landmarks. The results of Heinroth & Heinroth (1941) and Platt & Dare (1945) supported this view. The work of others, Thauziés (1910), Rivière (1929), Gibault (1930) and

Grundlach (1932), suggested that Pigeons were not entirely restricted to one-direction homing, but the data were limited or otherwise unsatisfactory. Similarly no great emphasis could be placed on fairly frequent reports of Pigeons homing from novel directions as a result of accident or emergency, as, for example, those listed by Osman (1950) and Kramer (1953*b*). Finally, however, Matthews (1951*b*) was able to show that pigeons of good stock could ignore a fairly rigorous directional training and give good homing from points at right angles or in the opposite direction. Kramer & St Paul (1952) also obtained good results with Pigeons that had been given a bare minimum of non-directional training. This evidence and its implications are more appropriately examined later (p. 44).

Birds other than Pigeons have seldom been used for message-carrying and hence their homing ability was subject to little experimental investigation until comparatively recently. Pliny (tr. P. Holland, 1601) tells us of a Roman race-horse owner, Caecina of Volterra who 'was woont to bring...a number of these Swallows...out of his friends' houses....And when (his) horses obtained victorie...would take the birds, and paint them with that colour which betokened victorie...knowing right well, that everyone would home to the same nest from whence they came.' Desbouvrie (1889) claimed to have developed a strain of messenger Swallows but appeared to be unwilling to demonstrate them. In the Pacific, Frigate Birds were long used for inter-island communication by the natives. During the last fifty years, however, there have been a large number of homing experiments, greatly varying in scale and value.

Many have taken place out of the breeding season, and particularly during the winter, when it is easy to trap large numbers of passerines with food-baited devices. Indeed, many small experiments were prompted by a desire to get rid of birds that persistently retrap themselves to obtain the readily available food. It is probable that a number of such experiments are unpublished or have only appeared in local journals. The data in Table 2 may therefore be incomplete. This lists the releases for thirty-five species, at no great distance from the point of capture, within an arbitrary limit of 25 miles. Return over such short distances would not seem to involve any special navigational

Table 2. *Short-distance homing experiments outside the breeding season*

(The distance in brackets is the farthest from which the birds returned when this is less than the maximum. Only birds returning the same season are included.)

Species	Used	Returned	Distance (miles)	Sources
Kestrel	?	?	?–20	19
Valley Quail	27	0	½–5	33
Moorhen	27	2	10–25 (15)	16, 27
Coot	?	?	?–25	16
Common Gull	2	1	19	23
Black-headed Gull	25	5	6–19	23
Swift	1	1	20	1
Middle-spotted Woodpecker	1	1	2½	36
Nuthatch	1	1	2½	36
Rook	90	3	19	9
California Jay	19	4	3½–4	33
Great Tit	452	115	½–28 (6½)	5, 8, 14, 18, 36
Blue Tit	119	49	½–28 (6½)	5, 6, 14, 18, 36, 37
Marsh Tit	6	4	½–4½	8, 18
Chickadee	32	17	1½–2	2, 22, 34
Pallid Wren Tit	16	0	3½–4	33
California Thresher	13	0	3½–4	33
Blackbird	11	2	1–9½	7, 13, 18, 24
Black Redstart	4	3	3–9	24
Robin	21	5	½–9 (1)	24
Hedge Sparrow	6	4	½–3½	18, 37
Baltimore Oriole	3	3	3	38
Greenfinch	11	11	1–10	11, 12
Siskin	4	4	1½–2½	15
House Finch	6	1	3½–4	33
Chaffinch	39	16	1–19 (5)	20, 28
Yellow Hammer	51	11	1½–7½	28
San Diego Towhee	35	7	½–4	33
Anthony Towhee	50	0	3½–4	33
Gambel Sparrow	148	29	3½–4	33
Golden-crowned Sparrow	42	13	3½–20	33
Fox Sparrow	3	1	3½–4	33
Song Sparrow	32	10	3½–15	17, 33, 38
House Sparrow	152	3	3½–9½ (7½)	3, 28, 36
Tree Sparrow	71	10	1–17 (7)	5, 28, 30, 36

Sources for Tables 2 and 3

1 Bertsch (1936).
2 Butts (1931).
3 Cohen (1948).
4 Creutz (1941).
5 Creutz (1949*a*, *b*).
6 Delmée (1940).
7 Dupond (1939).
8 Hämpe (1936).
9 Harrison (1934).
10 Hilprecht (1935).
11 Kenrick (1935).
12 Kerr (1936).
13 Koopman (1935).
14 Krätzig (1939).
15 Longpré (1935).
16 Mackworth-Praed & Gilbert (1936).
17 Manwell (1936).
18 Marples (1932, 1933).
19 Michner (1938).
20 Mennig (1935).
21 Montu (1941).
22 Odum (1941).
23 Petersen (1953).
24 Rüppell (1934*a*).
25 Rüppell (1937, 1940, 1948).
26 Rüppell & Schifferli (1939).
27 Scott (1949).
28 Schifferli (1936, 1943*a*).
29 Schifferli (1953).
30 Simon (1936).
31 Sumner (1936).
32 Sumner (1938).
33 Sumner & Cobb (1928).
34 Wallace (1941).
35 Warren (1929).
36 Wenkel (1935).
37 Wilson (1925)
38 Wood (1931).

Table 3. *Long-distance homing experiments outside the breeding season*

Species	Used	Returned	Distance (miles)	Sources
Buzzard	1	1	50	21
Goshawk	28	3	87–372 (124)	25
Kestrel	?	?	?–40	19
Moorhen	26	2	30–105 (90)	27
Coot	83	6	372	26
Common Gull	46	0	93–372	23
Black-headed Gull	243	20	93–434	23, 26
Cape Barn Owl	1	1	60	35
Rook	140	2	65	9
Alpine Chough	106	?	27–58	29
Great Tit	40	0	155–290	5, 10
Long-tailed Tit	1	0	130	10
Pallid Wren Tit	1	0	34	33
Blackbird	269	19	130–290	10
Hedge Sparrow	24	0	130–290	10
Greenfinch	554	21	130–310 (260)	10
Goldfinch	112	1	130–290 (130)	10
Chaffinch	423	1	62–290 (130)	4, 10, 28
Yellow Hammer	66	1	43–290 (130)	10, 28
Anthony Towhee	1	1	34	33
Golden-crowned Sparrow	35	2	34–84	31, 33
Song Sparrow	9	1	34–35	17, 33
House Sparrow	84	0	40–62	28
Tree Sparrow	67	0	30–186	5, 28

problems and can easily be attributed to a simple search for known landmarks. Nevertheless, the proportion observed to return is generally low. It must be remembered that at these times the birds may have been passing through the trapping area and so have no cause to return to it. A large proportion may have been birds of the year with as yet no fixed winter home. Even if the bird returns it is not necessarily attracted to the exact point of trapping and the chances of it being observed again, let alone retrapped, are accordingly reduced. These limitations also apply to those winter experiments in which twenty-four species have been released at greater distances (Table 3), and which would involve a real test of navigational ability. It will be seen that returns were seldom as high as 10 %, and were generally far fewer. The fact that any birds got back is in its way remarkable, since this often involved flying northwards in the middle of winter, such as in the case of a Black-headed Gull returning from Zürich to Berlin. But the overall results could easily be explained by chance factors. In many cases marked birds were still to be seen around the point of release weeks or months later. These winter homing experiments are thus of little value one way or another, they neither give definite evidence of navigational ability nor effectively deny it.

All the critical work in this field has therefore been done with breeding adults. Then, if the bird returns to the breeding area, it will be constrained to visit the nest. Watch can thus be concentrated and arrangements can often be made to retrap the bird. The birds used for such experiments should be robust enough to withstand handling and a long, generally foodless, outward journey in a small dark box. Incubation should be shared by the sexes, so that the nest will remain functional and attractive during the homer's absence, and should be prolonged so as to extend the experimental season. A nest in a burrow is additionally protected against predation and pilfering, and makes easier the catching and retrapping of the homing bird. If the birds nest in colonies, the collection of an adequate number is facilitated, and one watcher can keep a check on many nests. The Manx Shearwater, for instance, is clearly an excellent experimental animal for this purpose; nesting colonially in burrows, sexes sharing an incubation of 53 days, and capable of remaining on the nest for a fortnight, with an egg whose advanced embryo can withstand chilling for at least a week (Matthews, 1954). The homers are always marked individually with the numbered aluminium leg-rings, and the only unequivocal proof of return is when the bird has been caught and its number checked. Where this is not feasible, individual identification is still possible by means of codes of coloured leg-rings and/or plumage marks made with quick-drying paint. Watch is maintained, as continuously as possible, during that part of the day in which the birds are active at the nest. Griffin (1952*a*) has used, on a small scale, a radio-active 'watcher'. He attached a source of *gamma*-rays to a bird's leg-ring and placed in the nest a Geiger counter connected to a recording device. However, in most cases it would probably be cheaper to employ a human watcher.

Table 4 lists the short-distance releases of breeding birds of thirty species. Again returns from such small distances do not imply any particular navigational ability. Nevertheless, they do provide controls for the long-distance tests, particularly as to the efficiency of the watching systems. It will be seen that for most species the proportion of returns that were observed is high, giving confidence in the technique of checking employed. For the Red-winged Blackbirds and Cowbirds only about half were observed back. This may be because, although breeding, the birds were caught in food traps and not taken from the nest (of necessity in the case of the Cowbirds), and the disadvantages of such methods mentioned above still apply. The House and Tree Sparrows gave only 10% returns partly for the same reasons, but probably also because they were actually unable to return from more than very short distances. Table 5 lists the crucial long-distance experiments with breeding birds, which provide not only tests of navigational ability but the conditions in which its reality could well be demonstrated. Because of their basic importance these experiments are listed in full detail both of the thirty-four species and of the fifty sources, since different experimenters have different watching techniques, and use birds from different areas and in different conditions. The most valuable contributions are those in which large numbers of birds have been used from considerable distances—petrels,

Table 4. *Short-distance homing experiments during the breeding season*

(In addition returns from 'a few kilometres' with Nuthatch, Great Tit, Marsh Tit, Redstart, Greenfinch and Chaffinch have been reported; Witte, 1941.)

Species	Used	Returned	Distance (miles)	Sources
Leach's Petrel	64	46	1–25	12
Manx Shearwater	40	36	1–4	27
Gannet	4	4	1–10	16
Cormorant	2	0	2–10	26
Great Black-backed Gull	1	0	2	26
Lesser Black-backed Gull	24	20	1–20	26
Herring Gull	27	25	1–22	11, 13, 26
Common Tern	8	0	2–4	6
Arctic Tern	9	9	3–22	7
Sooty Tern	4	0	1	42
Noddy Tern	12	11	1–20	42
Swallow	53	47	4–28	18, 21, 22, 29, 46, 47
Rough-winged Swallow	2	2	4–7	10
House Martin	9	5	7–14 (9)	41, 46
Sand Martin	19	7	4–23 (22)	17, 22, 39
House Wren	14	9	¼–3	1
Blackbird	6	2	1½–9	2, 29
Robin	7	0	9	29
Starling	16	10	1½–22 (9)	22
	122	?	3–6	29, 30
Red-winged Blackbird	57	25	2–25	24
Cowbird	130	78	2–24	9, 28, 50
Chaffinch	3	1	2½	25
Sierra Junco	50	10	1½–6	4, 25, 40
House Sparrow	17	2	½–8 (6)	48
Tree Sparrow	56	6	1–20	5, 48

SOURCES FOR TABLES 4 AND 5

1 Baldwin & Bowen (1928).
2 Bierens (1936).
3 Buss (1934).
4 Cohen (1948).
5 Creutz (1949*b*).
6 Culemann (1928).
7 Dirksen (1932).
8 Fox (1940).
9 Gillespie (1930).
10 Gillespie (1934).
11 Goethe (1937).
12 Griffin (1940).
13 Griffin (1943).
14 Griffin (1952*c*).
15 Griffin & Goldsmith (1955).
16 Griffin & Hock (1949).
17 Jolley & Storer (1946).
18 Keller (1926).
19 Kluivjer (1935).
20 Lack & Lockley (1938); Lockley (1942).
21 Lippens (1935).
22 Loos (1907).
23 Lyon (1935).
24 Manwell (1941).
25 Marples (1933).
26 Matthews (1952*a*).
27 Matthews (1953*d*, 1955*b*).
28 Neff (1943).
29 Rüppell (1934*a*, *b*).
30 Rüppell (1935, 1936, 1938).
31 Rüppell (1937).
32 Rüppell & Schein (1941).
33 Schifferli (1942, 1951).
34 Spaepen & Dachy (1952, 1953).
35 Spaepen & Frangière (1952).
36 Stimmelmeyer (1930).
37 Stimmelmeyer (1932).
38 Stoner (1952).
39 Storer (1948).
40 Sumner & Pierce (1927).
41 Theinemann (1931).
42 Watson & Lashley (1915).
43 Wimsatt (1940).
44 Witte (1941).
45 Wodzicki *et al.* (1938, 1939).
46 Wodzicki *et al.* (1934).
47 Wojtusiak *et al.* (1937, 1946).
48 Wojtusiak *et al.* (1947).
49 Wood (1931).
50 Wood (1952).

Table 5. *Long-distance homing experiments during the breeding season*

Species	Used	Returned	Distance (miles)	Sources
Leach's Petrel	160	98	65–470	12
Storm Petrel	10	2	125–1000 (340)	20
Manx Shearwater	40	17	125–3050 (930)	20
	696	463	65–3050	27
Gannet	24	14	66–213	16
Cormorant	7	0	95–260	26
Man-of-war Bird	4	1	65	42
White Stork	25	13	30–1677 (1410)	45
Mallard	1	1	560	3
Peregrine Falcon	1	1	60	43
Semi-palmated Plover	4	4	50–70	14
Great Black-backed Gull	4	1	95–335 (95)	26
Lesser Black-backed Gull	225	136	30–515 (420)	26
Herring Gull	13	12	47–276	11
	164	152	62–872	13
	88	34	30–515 (315)	26
Black-headed Gull	6	1	70–185	26
Common Tern	80	36	94–456	13
	166	11	41–72	15
Arctic Tern	17	11	35–254	7
Sooty Tern	53	23	66–1300 (850)	42
Noddy Tern	66	33	45–1300 (850)	42
Puffin	6	2	125	20
Swift	21	10	150	34
Alpine Swift	36	12	1000–6200 (1000)	33
	5	3	250	35
Wryneck	19	6	211–930	31
Swallow	1	0	155	22
	2	1	46–109 (46)	18
	56	21	242–1150	29, 30, 31
	86	70	28–409	45, 46, 47
Rough-winged Swallow	1	1	33	10
House Martin	26	7	316–450	29, 30
Sand Martin	16	6	31–142 (67)	17, 39
Redstart	1	1	273	37
Bluethroat	20	2	273	36
Red-backed Shrike	12	1	223–745	31
Starling	802	226	40–1150	29, 30, 32
	33	11	93	19
Red-winged Blackbird	76	13	30–210	41
Cowbird	7	7	630–1200	23
	4	4	80–184	8
	28	11	32–110 (80)	28
	1	1	60	38
	2	2	56–100	50
Song Sparrow	1	0	75	49
Field Sparrow	38	0	30–186	5

shearwaters, gulls, terns, Swallows and Starlings—for only then can results be assessed with statistical confidence. Many remarkable individual returns have been achieved, and it is a pity that limitations of space prevent any detailed account of these. Some are illustrated in Fig. 6. Far and away the most outstanding homing feat has been that of a Manx Shearwater,

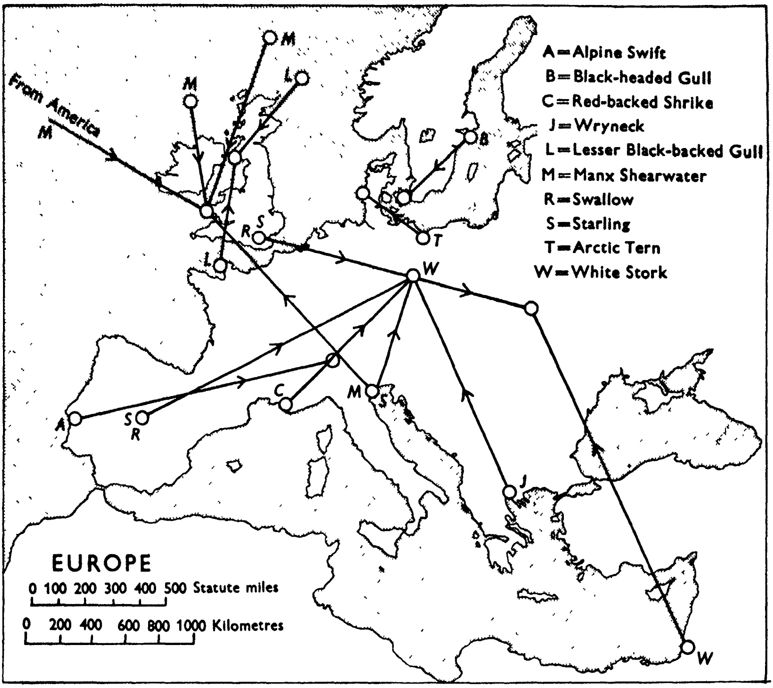


Fig. 6. Some of the longer, successful homing flights of European birds.

AX 6587, from Skokholm Bird Observatory, Wales (Matthews, 1953*d*; Mazzeo, 1953). This bird and one other were taken by air to Boston, U.S.A., a great circle distance of 3050 miles. The species is only known as a very rare, accidental straggler to North America. On 16 June 1952 at 01.30 hr. B.S.T. it was recovered in its burrow on Skokholm. Not until 10 hours after this did a boat come from the mainland, bringing mail which confirmed that this bird alone (its companion unfortunately died) had been released at Boston, 12½ days previously. But while it is justifiable to marvel, it is important to remember that isolated events are not in themselves sufficient to warrant the erection of any theories of special orientation or navigation. The extraordinary quirks of chance must be borne in mind and the overall results examined to check whether the more outstanding feats are really extreme examples of a normal navigational ability.

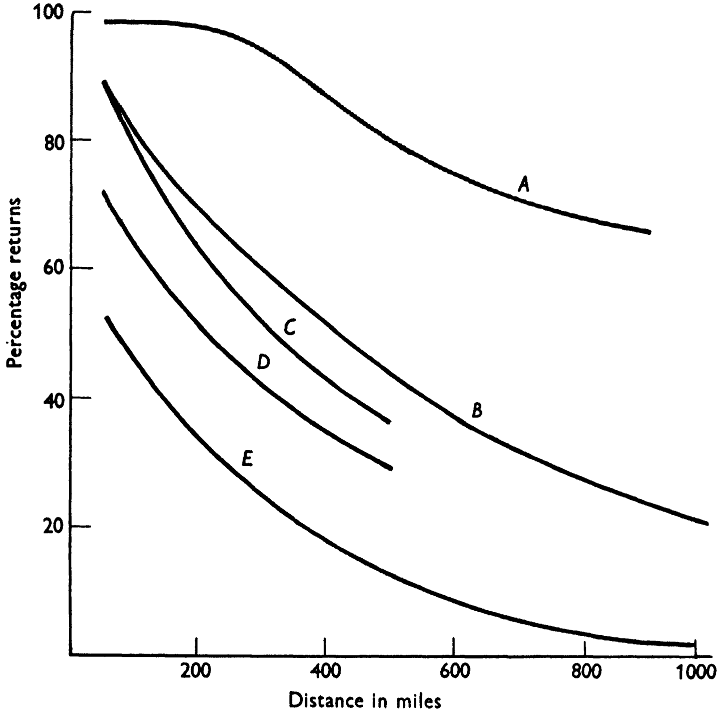


Fig. 7. Actual decline in percentage returns of homing birds with increasing distance of release. Various authors, see Table 5. Smoothed curves from collected data in Matthews, 1948. Herring Gull (*A*), Swallow (*B*), Common Tern (*C*), Leach's Petrel (*D*) and Starling (*E*).

There are features of the pre-war homing experiments (up to those of Griffin, 1943) which lead to suggestions that homing was accomplished simply by exploration. That the proportion of returns in most cases fell off rather sharply with distance (Fig. 7) did not necessarily imply the lack of a true navigational ability. Any non-navigational factors causing failure to home would have more time to operate on the longer journeys. More important was the fact that the speed at which the birds returned was, on the average, very low. The birds only covered as many miles (measured on the straight line for home) in a day as they could have done by flying straight for a few hours (Table 6).

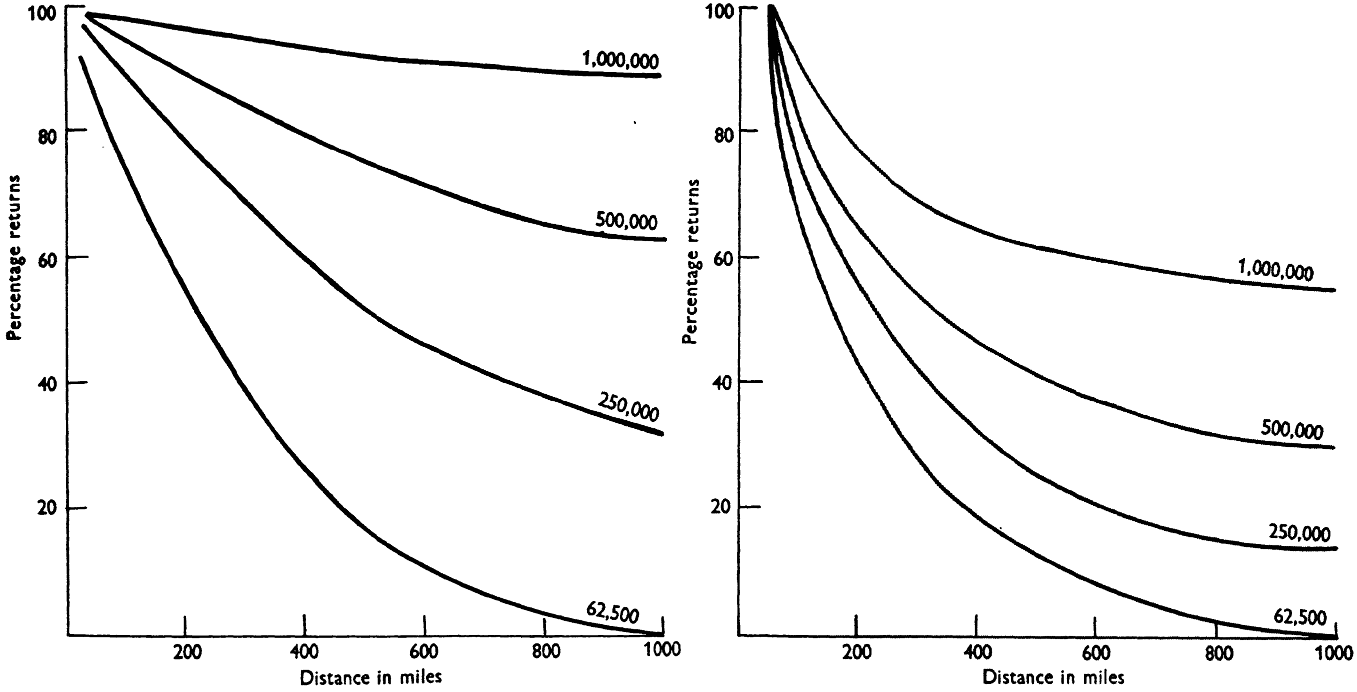
Table 6. *Speed of return from releases at 200–600 miles*

Species	No. of returns	Average speed in miles per day
Leach's Petrel	47	28
Herring Gull	96	73
Common Tern	23	130
Swallow	19	126
Starling	56	24

This suggested that the excessive time taken to reach home was, in fact, mainly occupied by flight in search for known landmarks, involving the coverage of great distances. This idea appears to have originated from observation on the behaviour of Homing Pigeons at release. Their habit of circling the release point led to the suggestion that 'they direct their flight in circles . . . a constantly increasing circle being made till they ascertain some known object enabling them to shape a direct course' (Rennie, 1835). This circular, or more properly, spiral search, has also been supported by Tegetmeier (1868), Hodge (1894), Grundlach (1932), and Heinroth & Heinroth (1941). It is probable, and in the case of the Heinroths, certain, that such a view was derived from a study of releases at relatively short distances, where, as we shall see later (p. 77), the more subtle forms of navigation are apparently inoperative. With spiral search the same proportion of birds should return despite an increase in the distance of release, whereas the average speed of return should decrease very rapidly. This is not the case. Moreover, to fly a regular spiral over great distances would in itself require a high degree of navigational skill—an objection that applies to any type of systematic search such as the rectangular search or expanding search suggested by Griffin (1952*c*). Simple radial scatter from the release point followed by continued flight in that initial direction taken at random, would only give a reasonable proportion of returns at short distances from a large 'target'. The potentialities of a completely random search for a known area were not fully appreciated until Wilkinson (1952) published his elegant mathematical analysis. The following summary of his assumptions and conclusions does less than justice to this paper, and in particular no attempt is made to discuss the mathematical treatment involved.

Wilkinson assumes that 'the mode of random search is to fly in a straight line for a certain distance, then turn, all angles of turn being equally probable, then fly another stretch in a straight line, turn again and so on'. He also assumes that 'the search effectively lasts only a finite time'. These assumptions are represented in the factor kt_0. k is the 'diffusivity' and, provided that the length (L) of the straight line flights do not vary excessively about their mean, $k = \frac{1}{4}vL$ where v is the flight speed in miles per hour. k is thus expressed in miles squared per hour, or as throughout Wilkinson's paper, as miles squared per day—that is to say, per 24 hours' flying time. t_0 is the period in days (24 hours' flying time) for which the bird will continue its search. It is reasonable to assume that this will be only a fraction (l/f) of the full time between release and giving up, since the bird must rest, eat and sleep. Wilkinson proposes an actual search of 8 hours per day making the full period of search three times that of t_0. L is an important factor. As it decreases so will the rate of turning per unit time increase, and the longer will it take the bird to wander away from the release area, although exploration will be more thorough. In general Wilkinson considers L as a flight constant of the species, but he does make calculations for a decreased L in familiar but not wholly known territory. We then have a direct analogy with the kinesis type of 'orientation' in the lower animals. kt_0 is thereby reduced, and likewise the probability of homing, for the greater the diffusivity the greater the chance of return in a given time.

Wilkinson considers two situations, homing along a narrow strip of coast and homing within a large land mass. The first is of less interest since if the home is on that coast there is a 50 % chance of return if the bird perseveres in one, randomly chosen direction along the coast. The assumption of random turns at



(*a*) (*b*)

Fig. 8. Theoretical decline in percentage returns of homing birds with increasing distance of release, on a basis of random search. (*a*) Along a bounded coast; (*b*) within a bounded continent. Relevant value of kt_0 shown on curves. (After Wilkinson, 1952.)

intervals in fact lowers the probability of return at the greater distances. The assumption that once a sea-bird has reached a coast it will confine its search to it may seem reasonable, but would not allow the bird to break away from one land mass to search another. Wilkinson also introduces the 'convenient fictions', a bounded coast and a bounded continent. As they are not vital to his argument, we may accept them for the present. Fig. 8*a* gives the relation between the distance of the release point from home and the probability of return for random search at several values of kt_0 along a coastline extending a thousand miles on either side of home. Fig. 8*b* gives the same relation for birds released in a circular continent of a thousand miles radius centred on home, which is itself surrounded by a circle of well-known territory 50 miles in radius. This latter is probably over-generous, but Wilkinson shows that in one example its reduction by a factor of 8 reduced the percentage return only by a factor of 1·75.

These theoretical curves may be compared with the actual results of the pre-war experiments shown in Fig. 7. Curves *A*, *C*, *D* are for sea-birds and may be compared with Fig. 8*a*, while curves *B* and *E* are of land-birds and more appropriately compared with Fig. 8*b*. It will be seen that there is a striking correspondence between the actual and theoretical curves. But we must inquire whether the values of kt_0 needed to produce this correspondence are reasonable. We can allot upper values to several of the component factors with some confidence. Thus $v=40$ m.p.h. and $f=3$ are plausible figures. t_0 is governed not only by the perseverance of the bird but also by that of the watcher. We may safely assume that systematic watch is not maintained after a month has elapsed, corresponding to a value of $t_0=10$. L is more uncertain. Using the above values for the other factors, the values of kt_0 on the curves in Fig. 8 require L to be successively 26, 104, 208 and 416 miles. Now considerations of visibility and the earth's curvature will limit a bird's horizon to about 20 miles. It does not seem reasonable to assume that a bird searching diligently for visual landmarks will fly 400 or even 100 miles in a straight line before making a turn on to a new course. From the limited data on flight paths of Gannets (Fig. 9) provided by Griffin & Hock (1949), Wilkinson derived a value for L of about 40 miles, giving kt_0 on the present values of 96,000. However, for the same data, since t_0 was much less than we have been assuming, the kt_0 value was only 18,000. Of the curves in Fig. 8, then, only the lowest, for kt_0 62,500, would seem to be at all reasonable. Even with this restriction it will be seen that the actual curves for the Starling and Common Tern show a close approximation to the calculated random curve.

Wilkinson also showed the falsity of the assumption that random search must result in a falling average speed of return with increasing distance of release. This would only be true if all the birds returned, whereas the proportion returning falls away with distance. Birds homing slowly (for whatever reason) will be able to return from short distances, but not from the more distant points, before watch is discontinued or the 'drive' to home peters out. The random search hypothesis is able to reproduce the independence of average homing speed with increasing distance, or even its increase, which were common features of the earlier experimental results. Return speeds of about the right order are demonstrated, and—another observed feature—a gap between the time of release and the onset of returns considerably longer than the minimum straight-line flying time.

Thus, while the higher values of kt_0 appear to be unreasonable, many of the earlier homing experiments appear quite consistent with random search. But as Wilkinson cautiously points out 'this agreement may not be interpreted as proving that random search is the mechanism of, or a large factor in, bird "navigation"....What it does show, however, is that these experiments...cannot be made to yield any information at all about the existence of a real navigational ability.' An important point that should be stressed is that the calculations assume that every bird reaching home is recorded and at the time it does so. In the actual experiments this seldom holds, both returns and speeds recorded are minimal. But clearly any new evidence must be subjected to searching scrutiny before it can be accepted as proof of the reality of bird navigation.

Attempts have been made to develop more refined methods to throw light on the homing journey and to determine how much of the time between release and return is actually spent in flight. There have been several suggestions (Brooks, 1945; Lack & Varley, 1945; McKay, 1945; Buss, 1946; Hecke, 1946) that radar could be used for following the birds. There is no doubt that micro-wave equipment can pick up small flocks of birds or even fairly large individuals. The 'echo' of the homing bird could be enlarged by various methods, but unless it could also be rendered unique there would be no certainty as to what was being followed. This would require a responder beacon mounted on the bird, and even with the latest lightweight equipment only very large birds, Albatrosses and Swans, could carry the load. The range of the detecting equipment is also limited when the birds are flying at only a few hundred feet, so that a network of receivers would be required, a condition unlikely to be fulfilled. Exner (1905) attached open-ended tubes containing camphor to Pigeons. The rate of evaporation of the camphor was increased by a flow of air and so, by weighing the tube on the bird's return, he hoped to measure the time spent in flight. But the evaporation was influenced by other factors such as temperature, and by the winds encountered on the ground and in the air, so no reliable results were obtained. Wilkinson (1950) devised a more refined form of flight recorder. This was essentially a small closed cylinder with, at one end a source of radioactive *alpha*-particles, and at the other a sensitive photographic emulsion. The particles impinging on the emulsion make discrete tracks which could be developed. For a given source strength the number of tracks (counted under the high power of a microscope) was a direct measure of the time of exposure. Between source and emulsion was interposed a ball-shutter which only opened when the cylinder was horizontal. The cylinder was attached in such a way that it was horizontal when the wing was spread in flight, hence the time in flight would be measured. Unfortunately, in practice (Matthews, 1953*d*) the device has been found to have a number of snags, particularly the recording of spurious 'flight' time and non-uniform decrease in source strength, which have greatly reduced its usefulness.

There have been attempts to follow birds from slow-flying light aircraft, namely Herring Gulls (Griffin, 1943), Gannets (Griffin & Hock, 1949) and Pigeons (Hitchcock, 1950, 1952;

Matthews, 1951*b*; Yeagley, 1951; Griffin, 1952*b*). A fair amount of success has been reported but the technique is a difficult one and the skill of the pilot is of paramount importance. The aeroplane itself does not appear to have affected the birds' flight, provided it flew well above them, but the possible effects of such interference must be kept in mind. An outstanding achievement was the tracking of nine individual Gannets for periods of up to 9 hours (Fig. 9). These few tracks certainly have the appearance of a searching type of homing, but there is a possibility of the birds having been baulked by high hills in the

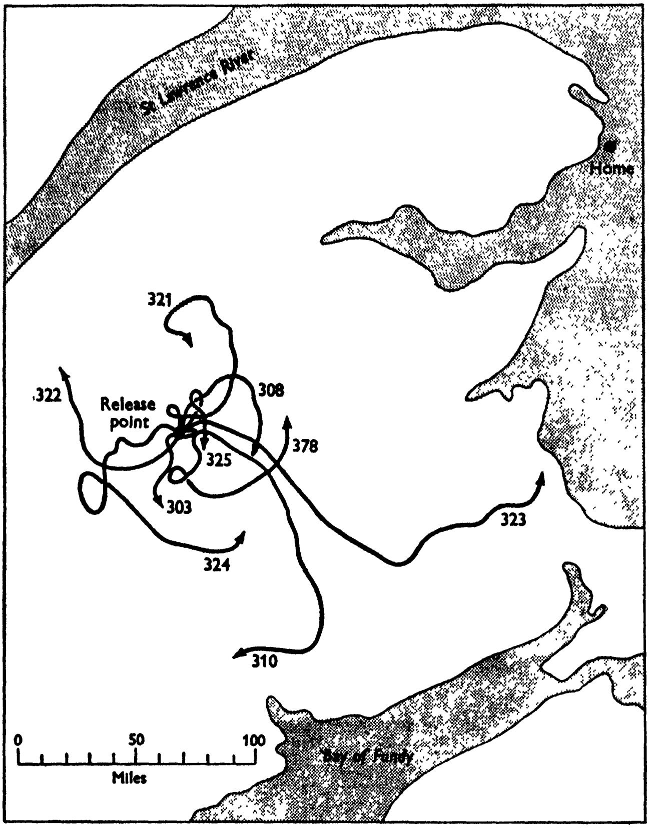


Fig. 9. Flight paths of homing Gannets as observed from an aeroplane. (From Griffin & Hock, 1949.)

direct line home. Also there is some suggestion from the observations that the birds were searching for suitable soaring conditions rather than for landmarks. With Pigeons it has been possible to follow fairly large flocks, but not small ones, a severe limitation in view of the variation in homing ability of individuals (p. 52). The results obtained have been largely confirmation of observations made from the ground, and have given small return relative to the time and money expended.

As we shall see in the next chapter the solution of the problem has been obtained by less exotic methods, by using homing conditions such that the apparent homing speed approaches the true homing speed, and by study of the behaviour at departure. This latter has generally been observed by the liberators but only in recent work has such observation been systematic. Each bird is watched out of sight with powerful binoculars and the point at which it vanishes (and the time taken to reach it) noted. This may be misleading as an indication of flight direction for the individual. For instance it may indicate the limits of a side-to-side movement, or an initial false start may have taken the bird so far that it is lost before its final heading approaches the same bearing from the observer. But with a large number of 'vanishing points' under a given set of conditions, a scatter diagram is built up whose orientation, or lack of it, can be accepted with statistical confidence. With two observers stationed some distance apart, cross-bearings can be obtained and so a better representation of the bird's actual track is reached.

CHAPTER 4

The Reality of a Form of Complete Navigation in Birds

AN alternative explanation of the slow homing speeds, which are an essential prop of the random search hypothesis, is that the birds are in fact aiming for home but fly for only an hour or two each day. Now the only previous occasions on which a wild bird would have made a long flight in one direction would be on migration. Some inferences might therefore be drawn from the latter type of behaviour. Field observations show that passerine migration does not continue evenly but is condensed into a short period of 3 or 4 hours each day (e.g. v. Hartmann & Bergman, 1943) or night (Siivonen, 1936; Lowery, 1951). This is confirmed by the study of migration-unrest in caged birds (Palmgren, 1949). Individual flights would be shorter than the overall period of movement, and we should expect such birds to cover only about a hundred miles a day. But it is not known whether the individual will travel every day; nor can an average daily coverage be determined from ringing recoveries, for there is small chance of a bird being killed or retrapped at a distance soon after being ringed initially. A few records available range from 44 to 510 miles per day. Southern (1941) having analysed the arrival dates of spring migrants throughout Europe and calculated the average speed at which a number of species advance, found that the fastest was the Red-backed Shrike, at 55 miles per day. This is a minimal figure since it is known that in many species birds breeding far to the north start later, and the same birds will not be continuously in the advance guard.

The sparse migration data do at least indicate that for many species migration proceeds at a leisurely daily rate, and may be taken as indicating that similar speeds will obtain in homing flights. Another factor reducing homing speeds would be delay in starting while the bird recovered from the effects of its forced journey. Thus Rüppell's Starlings were frequently observed to make for and perch in the nearest trees, while more than half the gulls released by Matthews near water landed, and remained, bathing and preening, for as long as observation could be kept. To eliminate such delay it would be necessary to release birds in situations such that they would be unwilling to alight—land-birds over the sea or pelagic birds over land. Soaring birds might delay their departure until suitable thermal conditions developed, or might actively seek them. Lastly, the species used should execute extensive migratory movements and/or range far afield while foraging. There were isolated instances of birds returning at speeds greatly in excess of the average, as listed in Table 7. But such results were quite exceptional and as they stand could easily be the result of chance. Moreover, in only two instances was the homing speed of the same order as the normal flight speed, and there is doubt whether these were released in unknown territory. Both were sight records only. The speeds of the birds not returning within the day could be increased by assuming a certain rest period, but to be really convincing the evidence would have to avoid the need of arbitrary assumptions. The Manx Shearwater is a bird having all the requirements set out above for swift homing. It is exclusively pelagic, only coming ashore to nest, and is very clumsy on land. It is not a thermal soarer, and is a pronounced migrant, Welsh birds flying some 6000 miles to South America.

Table 7. *Instances of swift homing flights*

Species	Distance (miles)	Homing time (hr.)	Homing speed (m.p.h.)	Author
Manx Shearwater	125	10	13	Lack & Lockley (1938)
	200	24	8	Lack & Lockley (1938)
Gannet	213	24	8	Griffin & Hock (1949)
Herring Gull	104	3½	30	Griffin (1943)
Common Tern	404	37	11	Griffin (1943)
Swift	150	4	37	Spaepen & Dachy (1952)
Alpine Swift	1000	69	15	Schifferli (1942)
Swallow	240	27	9	Rüppell (1935)
	254	26	10	Rüppell (1935)

It also undertakes extensive foraging sorties of perhaps between 100 and 300 miles while breeding (Lockley's claims (1953) that such birds go as far as 600 miles from the nest are without adequate foundation). Further experiments with this species were therefore carried out by Matthews (1953*d*, 1955*c*). It has one drawback in that, although a diurnal bird, it returns to its burrow only after dark, presumably to avoid predation by the larger gulls. This means that birds arriving back off the island must wait for perhaps many hours before landing.

Table 8. *Distribution of Shearwater returns, sunny conditions early in the season*

Nights after release	1st	2nd	3rd/4th	5th/10th	Later
Returns	15%	38%	27%	13%	7%

Of 152 released in sunny weather from mid-May to mid-June, conditions shown to be conducive to good homing, 131 (86%) are known to have returned the same season, giving the time distribution shown in Table 8. Thus more than half were back on the first two nights. Nineteen of these were actually back on the night following release, at the *minimal* speeds listed in Table 9. It will be seen that birds released late in the day at a considerable distance gave homing speeds approximating to the usual flight speed, unequivocal evidence of an almost direct flight from the unknown release point inland to home. Those released nearer and/or earlier in the day gave slower apparent speeds, and it is reasonable to suppose that this was because they actually reached the island long before they were able to land. Conversely it is probable that not all of the later releases were able to get back in time to effect a landing that night. Thus the morning release at the 265-mile point gave six first night and only two second night returns. When the same number of different birds, twenty, were released there on another occasion but in the evening, 19.45 to 20.40 hr., there were not any returns that night, but thirteen arrived on the second. It seems very probable, therefore, that many of the fifty-one birds arriving on the second night had homed very much faster than the extra 24 hours elapsed would suggest. The distribution of returns in Table 8 is also clearly very different from that which would be expected on the basis of random search.

This demonstration of straight-line homing in a wild bird paralleled earlier work with the domestic Homing Pigeon (Matthews, 1951*b*) in which it was shown that pigeons from good stock could ignore directional training and home from unknown points in novel directions. Thus in four such tests eighty-seven out of a hundred birds returned, and of these fifty-seven were back on the day of release at average speeds of 17·7, 22·6, 23·2 and 26·9 m.p.h. A further twenty-five were back the following morning. Similar results have been obtained in later tests (Matthews, 1953*a*, 1955*a*, *b*). Kramer & St Paul (1952) and Kramer (1953*a*) confirmed and extended this by using older birds given only a little non-directional training, released in groups 200 miles distant. In two tests thirteen groups gave a good proportion of returns at speeds averaging 25·8 and 38·5 m.p.h. Some doubt is cast on these returns, however, by the release with them, or shortly after and before, of other Pigeons that had received training from that direction or had actually flown from that point before.

Table 9. *Swift homing flights with Manx Shearwaters*

Distance (miles)	Time of release (B.S.T.)	Return speed (m.p.h.)
215	07.05–07.30	12, 12
155	07.31–08.33	9, 9
265	10.30–12.14	17, 18, 18, 19, 19, 20
235	15.16–15.34	22, 23
125	16.45–18.19	16, 16, 17
235	18.21–18.42	28, 29, 29, 35

It will be seen that the demonstration of straight-line homing from an unknown point is largely a matter of choosing the right birds and the right conditions. It is often tacitly assumed that every bird is striving equally to regain home, whereas there appears to be a wide variation in this factor. Pigeon fanciers are naturally much concerned with the problem, but the very multiplicity of their recipes for speedy homing indicates its complexity. It is clear that it is not essential for the Pigeons to be breeding, since young birds 3–4 months old home extremely well, while v. Oordt & Bols (1929) obtained good homing with castrated pigeons. The association of food with home is probably important, as shown by Matthews (1952*b*). In the course of learning experiments (p. 57) pigeons were introduced into, at first, entirely novel surroundings once a day and food was provided there and nowhere else. Some took food on the first day others not until the ninth. For thirty birds there was a strong correlation between this unwillingness to feed in strange surroundings and the homing ability previously demonstrated in field tests. It is possible to split the food/home association by training pigeons to feed in a conspicuously marked basket placed at some distance from the loft. Two-way homing can then be achieved over short distances; the birds will even fly to the food basket when released from an aircraft overhead.

It is undoubtedly true that mating and breeding increases the attraction to the loft, and it is almost impossible to settle mature birds in another situation. Cocks and hens appear to have equal merits as homers. There is much difference of opinion as to whether Pigeons race faster when returning to eggs, small young being fed on 'milk', or large young. It is quite probable that some individuals react best to one situation and some to another. Some fanciers practice the 'widowhood' system whereby the cock is deprived of his hen, then given a brief sight of her before being sent on a race, but prevented from copulating. That privilege is accorded him on his return. There are many other 'dodges' such as the provision of special titbits before and after a race. Pigeons will generally home faster when liberated in small groups or even pairs. It is probable that grouping satisfies the desire for company, which appears to be strong and may lead solitary fliers to join up with a foreign group, and so get led astray. Possibly the group introduces an element of competitive striving, and may lead to the cancelling out of diverging flight lines.

We naturally know even less about variations in the homing urge among wild birds. Despite the observational difficulties it would seem that the poor homing of birds taken from their winter quarters reflects a true difference from the results obtained with breeding birds. Unfortunately, there are no experiments using birds drawn from the same population in both their summer and winter homes. Matthews found a falling-off in homing results with the advancing season in Manx Shearwaters. Of eighty-two released in the second half of June in sunny conditions only fifty-three (65 %) returned that season, with the spread shown in Table 10. This is to be compared with the 86 % returns for releases between mid-May and mid-June, and with the data in Table 8. All the birds were taken from an unhatched egg. There may be a tendency to desert at later stages of incubation, but this would only account for the increase in failures. The slower returns might be interpreted as due to a falling-off of the homing urge and/or to a decline in general stamina with repeated periods of fasting, and with the onset of the moult. The latter affects the homing of Pigeons adversely. It was also shown with Shearwaters that swifter homing could be expected from birds which had just begun their incubation shift (which averages about 5 days) than from those shortly due for relief. Rüppell (1935) found that male Starlings gave a rather higher percentage of returns than did the females (33 % of 138 as against 25 % of 195), particularly at the beginning of the breeding season. The other species used in large numbers for homing experiments are unfortunately not readily sexed in gross examination.

Table 10. *Distribution of Shearwater returns, sunny conditions late in the season*

Nights after release	1st	2nd	3rd/4th	5th/10th	Later
Returns	2 %	24 %	36 %	36 %	2 %

Since direct homing has been demonstrated in two species and since it is probable that other species would give similar results with the right conditions, the determination of the exact homeward track becomes much less important. The poor dividends paid by the more exotic methods of study are thus less of a disappointment. There is a little information to be derived from recoveries and sightings of homing birds *en route*. These must be treated with some reserve in case of bias by an uneven distribution of competent observers. Also birds recovered dead may have been weakened and were not necessarily still trying to home, though this objection need not apply to birds shot or crashing into telegraph wires. There are only nineteen reports of birds found more than 25 miles from either release point or home, comprising eight Manx Shearwaters (Matthews, 1953*d*, and unpublished), two White Storks (Wodzicki *et al.* 1939), three Lesser Black-backed Gulls (Matthews, 1952*a*), two Herring Gulls (Griffin, 1943; Matthews, 1952*a*), one Sooty Tern (Watson & Lashley, 1915) and three Starlings (Rüppell, 1936, 1937). These recoveries and sightings are represented in Fig. 10, and support the conclusion of essentially directed flight. Two-thirds lie within 45° of the home bearing, and the average deviation for the whole scatter is only 47°. Ringing recoveries do not reveal how long the bird has been where it was found and so afford no indication of speed, but two Shearwaters and two storks recovered on the day after release had covered respectively 129, 150, 142 and 180 miles in the direct line. Directed homing is again evident in the recovery points of twenty partially trained and untrained Pigeons figured by Kramer (1952) and Kramer & St Paul (1954). All but two were within 45° of the home-bearing with an average deviation of 23°. Earlier experiments with untrained Pigeons such as those of Gibault (1930) had yielded six recoveries, all but one within 45° (Matthews, 1953*b*). It is interesting that eight recoveries in winter homing experiments, namely one Coot (Rüppell & Schifferli, 1939), one Common Gull and six Black-headed Gulls (Petersen, 1953) gave an average deviation of 78°, not significantly different from the random scatter value of 90°. This is in accord with the low homing returns in such experiments.

In view of the meticulous care with which percentage returns and average homing speeds have been recorded by many workers it is surprising that only recently have attempts been made to measure that other part of the homing performance open to observation, the behaviour soon after release. If no indication of homeward orientation were forthcoming this would not exclude all forms of navigation (p. 79). But if definite orientation could be repeatedly demonstrated in completely unknown areas, the case for navigation would be incontrovertible. Suggestions that such initial orientation occurred may be found in the work of Watson & Lashley (1915), Manwell (1936), Wodzicki *et al.* (1938), Schifferli (1942) and Wojtusiak (1949) but without sufficient statistical evidence. On the other hand Rüppell (1935) and Griffin (1940, 1943) failed to find indications of orientation. It is interesting to note that six of the nine Gannets followed by Griffin & Hock (1949), shown in

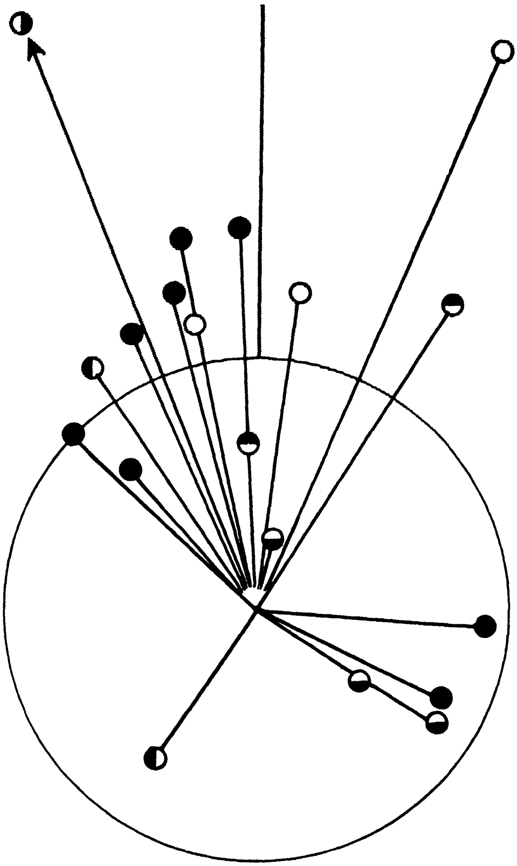


Fig. 10. Recoveries *en route* of breeding birds released in homing experiments. Results from various authors (see text) superimposed on one release point and about one home bearing (vertical line). The circle has a radius of 100 miles. A strong homeward trend is to be observed. ●, Manx Shearwater; ◓, White Stork; ◒, Lesser Black-backed Gull; ◐, Herring Gull; ◑, Sooty Tern; ○, Starling.

Fig. 9, *started* in the home direction despite their subsequent apparently random tracks.

Once again a positive demonstration awaited only the use of the right birds in the right conditions and in sufficient numbers. Matthews (1951*b*) was able to show a definite homeward orientation with Pigeons released off the training line at a previously unknown point in sunny conditions. Further confirmatory evidence has been published later (Matthews, 1953*a*, 1955*a*, *b*). It was clearly important that such a crucial point as this should be established beyond doubt, and that any possible bias due to topographical features, wind direction, etc., should be excluded. Accordingly a number of release points in various directions from the loft and in different types of country have been used (Fig. 11). A total of 340 compass bearings at which individually released Pigeons were lost from sight in binoculars are recorded in Fig. 12. Four head-, nine beam-, and three tail-winds were encountered in these tests. The average deviation from the home bearing was 47°, as compared with the random value of 90° and the minimum observed, by this method, 23° for birds released at a well-known point. Of the bearings 53 % were less than 45° off the home line, compared with the 25 % expected from a random scatter. There is every reason to accept the statistical verdict that the initial scatter of these Pigeons had a very marked homeward orientation. The fact that the birds were able to ignore the training direction suggests that the tendency to fly in one direction had not yet been imposed by the amount of training given. The previous orientation at unknown points on an extension of the training line can therefore be taken as further evidence of a true navigational ability. There are 212 of these bearings for seven separate experiments from six different points (1, 3, 4, 7 and 9 in Fig. 11). They give an average deviation of 44°; and 66 % are less than 45° from the home line. The fact that those Pigeons giving good performances on training line releases also did well in releases off that line confirms the assumption that the same orientation process was concerned.

We may conclude that, within the short time they were in sight, these Pigeons were able to determine the rough bearing of home, in the complete absence of any known landmark. This

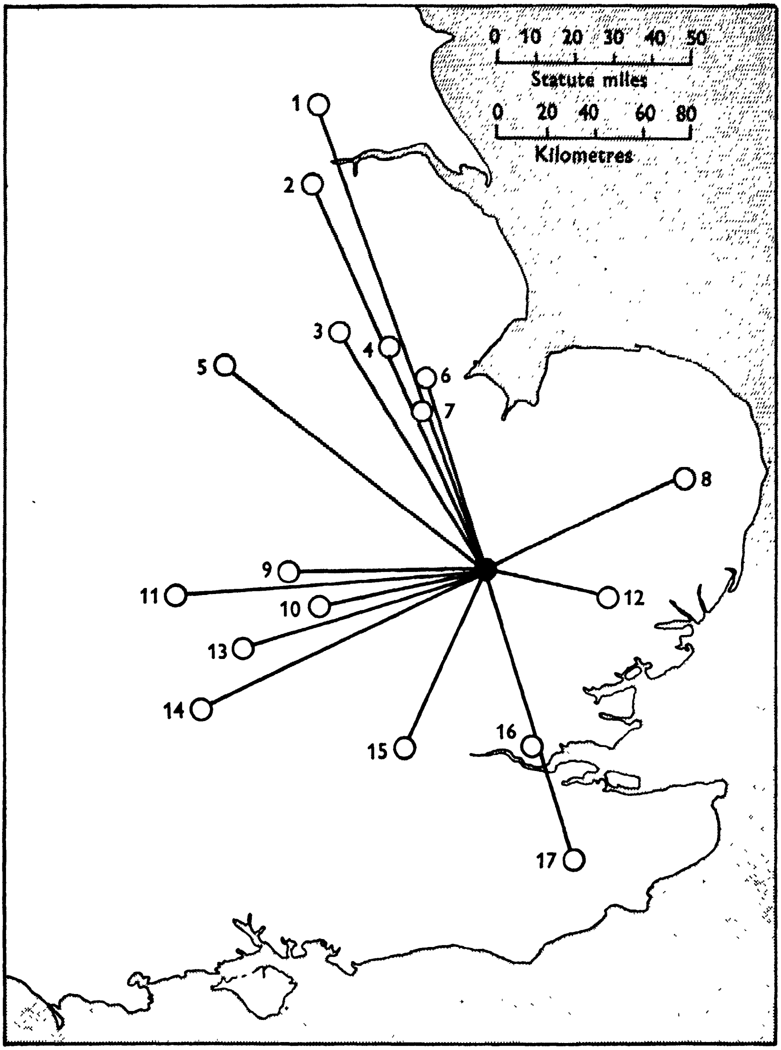


Fig. 11. Points at which Pigeons from lofts near Cambridge have been released. Only points more than 25 miles from the loft are shown.

'time in sight' has an important part in navigational theory as will be seen later (p. 111). Independent confirmation of an initial homeward orientation by Pigeons has been given by Kramer (1952, 1953*a*) using birds with only short-distance non-directional training released at an unknown point. He gives thirty-two bearings for three experiments at two points.

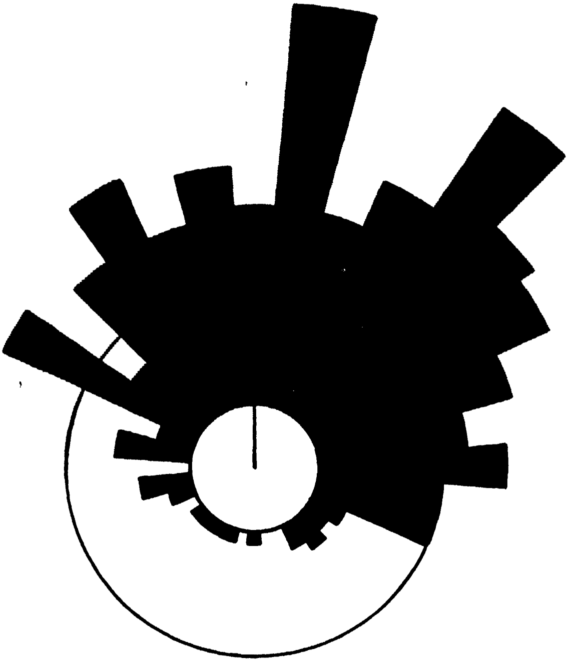


Fig. 12. Orientation of Pigeons at unknown points in novel directions, in sunny conditions. Results of sixteen experiments superimposed about one home bearing (vertical line), from points 2, 3, 4, 5, 6, 7, 8, 10, 13, 14, 16 and 17, in Fig. 11. Bearings of vanishing points are grouped in 10° sectors, the length and thickness of the rays being proportional to the number of bearings in each sector, being 10 when the circle is reached.

Initial homeward orientation has also been demonstrated in wild birds. The two species of gull used by Matthews (1952*a*) are not very suitable for the demonstration of orientation, which calls for the same qualities as those needed to give a likelihood of swift homing (p. 39). A large proportion landed soon after release, and they would be influenced by soaring conditions to some degree. Another difficulty, common to wild bird experiments, is that their release cannot be postponed indefinitely until good weather conditions supervene. Releases were distributed among a large number of points and liberators to avoid topographical and observational bias. Omitting releases in areas which ringing recoveries indicated might be familiar to the birds in the course of their seasonal movements, the bearings of forty-eight Lesser Black-backed Gulls were observed and are shown in Fig. 13. The average deviation is 2·7 compass points with 55 % within two points of the home bearing, compared with the random expectation of 4·0 and 31 %. The scatter is strongly orientated in the home direction. With the Herring Gull the equivalent figures were 3·2 and 50 %, also a homeward tendency, but, as it was based on only twenty-two birds, this cannot be considered as statistically significant. These homeward tendencies are all the more interesting since the decline of returns with distance, and the low average speeds of return obtained with these gulls, made their performance similar to those species used by Wilkinson to demonstrate the potentialities of the random search method. This is therefore definite evidence that poor homing performances need not imply a lack

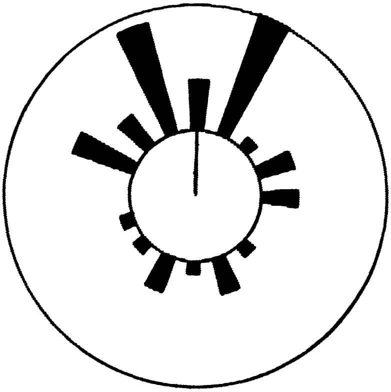


Fig. 13. Orientation of lesser Black-backed Gulls at unknown points, in sunny conditions. Releases from twelve different points superimposed. Bearings grouped to nearest compass point.

of orientation and may be due to a slow daily rate of progress towards home.

The Manx Shearwaters used by Matthews (1953*d*, 1955*c*) have all the qualities needed for a study of orientation behaviour. Again a number of release points were used (Fig. 14), all but one inland and hence unknown to this exclusively pelagic bird. The points were arranged in all directions from the colony except to the south where the coast would be well known to the birds, in case there was any directional bias by these birds when released inland. The exceptional point was on a weather ship in the open Atlantic, without any landmarks at all. Fig. 15 records

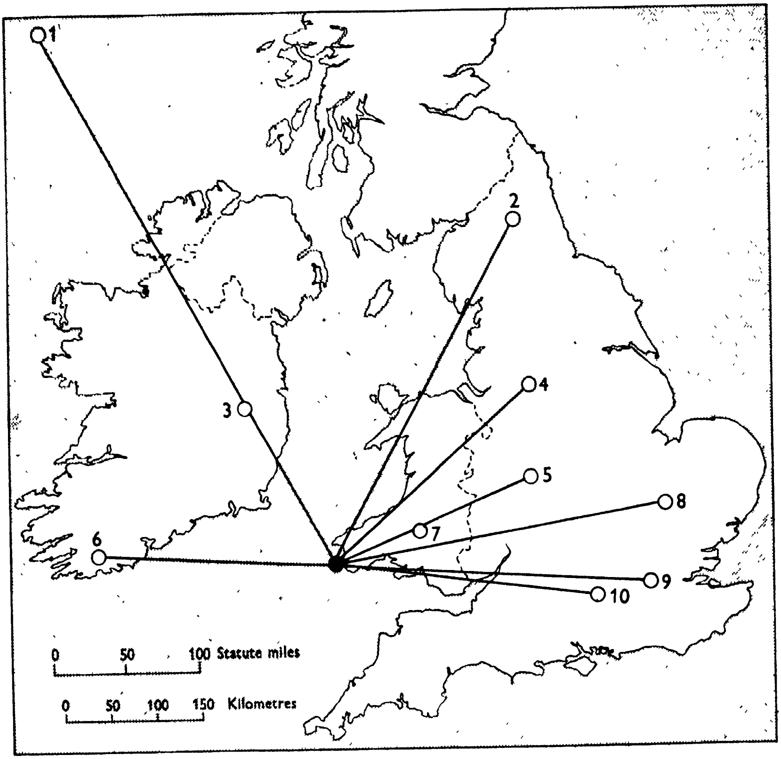


Fig. 14. Points at which Manx Shearwaters from Skokholm Island have been released.

210 bearings. The average deviation is 2·5 compass points with 62 % of the bearings within two points of the home *line*, *a very* strong orientation, similar to that obtained with Pigeons. It may be stressed again that these are the results obtained by a number of independent observers.

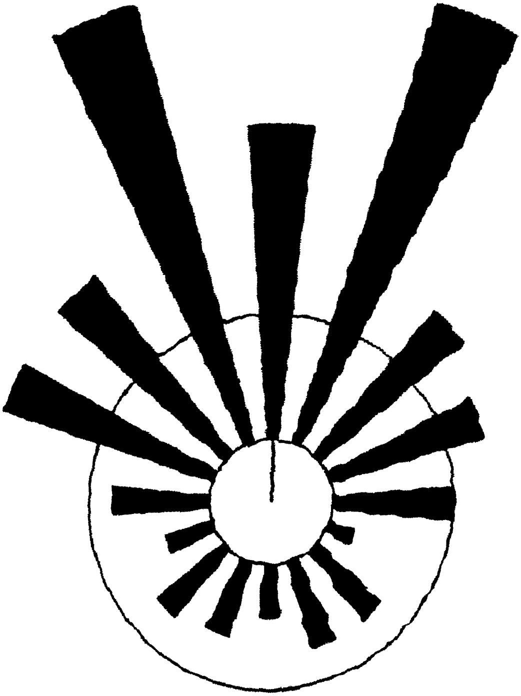


Fig. 15. Orientation of Manx Shearwaters at unknown points, in sunny conditions. Results for thirteen experiments superimposed, from points 1, 2, 3, 5, 8 and 10 in Fig. 14.

We thus have concrete evidence of *homeward* orientation in three very dissimilar species, and *suggestive* evidence for one other. Couple this with the concrete evidence for straight-line homing in two of the species and the case for the existence of a navigational ability is strong indeed. This is especially so since the Pigeon and Shearwater data are sufficiently extensive to show that there is a positive correlation between the initial orientation and the homing speed. Even the birds recovered *en route* (Fig. 10, p. 45) were in most cases on bearings close to those on which they were lost from sight.

Now, if we are dealing with a definite ability we are likely to find individuals with that ability developed to different degrees. It has long been a commonplace amongst Pigeon fanciers that some of their birds are faster and more consistent homers than others. But we have seen that the circumstances of pigeon racing place a premium on speed and stamina rather than on navigational ability. However, Matthews (1952*b*, 1953*b*) analysed the performances of over a hundred Pigeons in a series of critical tests covering nearly 500 sorties in good weather conditions. Each bird's performance was assessed in terms of two arbitrary indices: for accuracy of orientation and for swiftness of return. A wide range of individual indices was found, as shown in Fig. 16. It is just possible that using only random searching, certain Pigeons would consistently return faster than others—they might search more vigorously and have a better memory for landmarks. But the ability of some Pigeons to start off closer than others to the home bearing, time and time again, cannot be accounted for on any random basis. The distribution of the two indices is interesting; that for orientation approaches the form of a normal curve, which would result if we were dealing with a single quality (or group of interdependent qualities) ranging about the mean. On the other hand, the distribution of the return index departs strongly from normal and is of the form that would be expected if we were measuring the effects of a number of independent factors. It was further shown that birds with poor orientation ability produced poor returns. With moderate or good orientation ability the other factors governing the return assumed the greater importance. This is in accord with the view that the orientation mechanism is not of phenomenal accuracy, but sufficient to impart a homeward trend to the flight, home being pinpointed by pilotage rather than navigation. Variation between different stocks of Pigeons bred by different fanciers and tested under the same conditions was also demonstrated and this was confirmed by Pratt (1955). It appeared that in one particularly poor stock the readiness to become conditioned to flying in one direction only was marked. Failure to appreciate the wide range in navigational ability, the existence of 'bad' and 'good' stocks of Pigeons, has undoubtedly led to many of the conflicting results reported by different workers.

The difficulties of carrying out repeated releases at different points with wild birds are great, and in general far too few tests have been done for any assessment. The Manx Shearwater is again a suitable animal, returning year after year to the same burrow and mate, and having a long life. Of these birds 148 have now made two or more homing flights from different points each time, with a total of 358 sorties (Matthews, 1955*c*). Unfortunately, even this large sample is insufficient, since many sorties were in poor weather conditions. As far as they go, the indications are for the occurrence of individual variations, though less markedly than in Pigeons. The Shearwaters have, of course, been subjected to several years intense natural selection for such abilities before they were tested experimentally. In species where selective pressure on navigational ability is less marked, as in sea-birds that do not wander far from a coast, a wider range of individual abilities might be expected. Indirect evidence of such a variation was found in the Lesser Black-backed Gull (Matthews, 1952*a*), a constant proportion, about

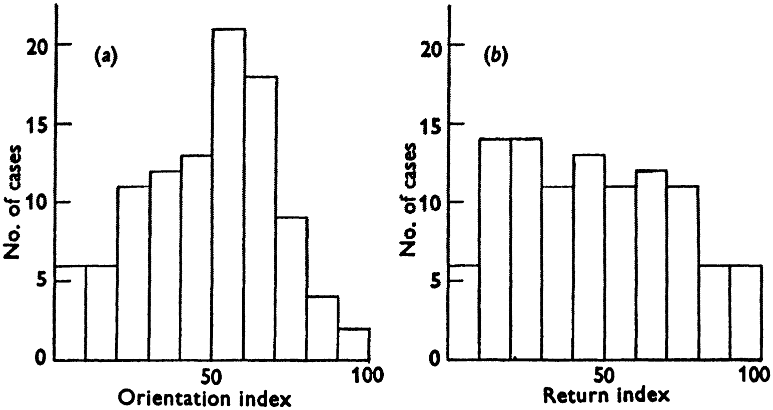


Fig. 16. Distribution of individual indices of accuracy of orientation and swiftness of return in Pigeons. (From Matthews, 1953*b*.)

20 %, homing relatively quickly whatever the distance of release. It may be pointed out here that well-developed homing behaviour is a necessary concomitant of territorial behaviour and hence shares the advantages of the latter—even spreading of the population, assurance of food supply, segregation during courtship, etc. Intraspecific competition is reduced by the avoidance of what might seem to be a natural tendency to settle in the first favourable area encountered on migration. Indeed, without homing all regular migration would break down. Then, again, having in effect only two home areas, many migrants spend their lives in a fairly limited range of ecological situations, an important consideration when behaviour is of a rather inflexible type. Lastly, there are the important genetical and evolutionary effects produced when local populations remain discrete breeding units.

In Britain, the Herring Gulls seldom move further than a hundred miles from their breeding grounds, unlike the Lesser Black-backed Gulls which are markedly migratory, moving from Scotland to West Africa. It is therefore interesting to find that the former, from the same colony as the latter and subjected to the same treatment, gave only 6 % of fast homers. In America, the Herring Gull used by Griffin (1943) is migratory and gave a much higher proportion. Experiments with completely sedentary wild birds have generally been outside the breeding season, when even migratory birds give poor results. The experiments with breeding birds have been confined to the House and Tree Sparrows, and these have given no returns from farther than 9 miles. The Homing Pigeon derives from non-migratory stock, the Rock Pigeon of the Middle East, and is still, of course, entirely sedentary. But artificial selection for homing ability has been going on for thousands of years and has become intense during the last hundred, replacing the selection which migration would impose on a natural population. It must be remembered, too, that migration is a somewhat flexible form of behaviour. Thus Lack (1943) showed that some individuals of a local population are migratory, others sedentary, while Nice (1933) found that the individual bird may change its status. We have seen (p. 12) that non-migratory stock can be readily induced to migrate by example. Differences in local populations, such as those of Herring Gulls, are common. Moreover long-term changes of status may occur, such as the increasing tendency for Lesser Black-backed Gulls in Britain to remain over winter, a return to the residential status with which they were credited in the nineteenth century. This raises the question of how the orientation mechanism and its sensory equipment could be developed in a sedentary species or remain, latent, in a sedentary phase. It is clear that if it is to be developed or retained against selective pressure, the sensory equipment would have to play a more general part in the animals' life. Postulates of extreme refinement of sensory equipment are acceptable only if it can be demonstrated that the earlier, cruder stages of development would have selective value, presumably for some purpose other than navigation.

The existence of variations between individuals and stocks in the ability to navigate carries the implication that part, at least, of the mechanism must be inherited. It was long thought that Pigeons could home well only after training, and the few reported cases of homing by untrained birds could be easily explained on the basis of chance. However, Matthews (1953*b*) showed that young Pigeons simply allowed their freedom to fly in the neighbourhood of their loft, showed a marked homeward orientation when released singly 50–75 miles from home. Thirty-two such birds released in three experiments at different places gave an average deviation of 53°, with 56 % within 45°, a performance but little inferior to the experienced birds. Similar orientation by untrained Pigeons have been reported by Kramer & St Paul (1954) and by Pratt (1955). The former reduced further the experience of their birds by keeping them in a large aviary, 6 × 10 × 3 metres high, up to the time of release. Returns were considerably poorer than those obtained with trained birds of the same age and stock, although recoveries were in the general direction of home (p. 44). Rüppell (1938) has reported the only comparable experiments with wild birds. He kept young Starlings in a large aviary over their first winter and, when they had started breeding the next spring, released them 70 miles away. None returned and there were several recoveries near the release point. Other Starlings that were similarly treated *after* they had migratory experience (Rüppell &

Schein, 1941), homed well from the same place. Unfortunately, there is no information about orientation at release, a vital point.

It would seem, therefore, that the orientation mechanism is innate and ready to function when first called upon. It is no part of our limited aim to attempt an explanation of the way in which such remarkable behaviour patterns can be inherited. This is one of the crucial mysteries of biology. It is sufficient for our purpose to note that many other equally complicated types of behaviour have been clearly shown to be inherited. Learning from experience must also play some part if the directions of the innate mechanism are to be followed to a successful conclusion. The factors concerned are likely to be psychological—'confidence' to fly over strange territory long enough to regain the loft, and to avoid joining strange flocks or foraging in strange lofts or in the fields—and topographical—the increase, by training flights, of the target of known area round the home loft. The essential information as to what *is* home must also be built in by a learning process. We have seen that young migrants have no innate information as to where their winter home actually is, and that they and young Homing Pigeons will readily adopt a foster home.

Another assumption in random search theories is that birds are quick to memorize and recognize visual landmarks. An area many miles across is credited as known territory, likewise ground covered on migration or previous homing flights. The implication of a photographic and virtually inexhaustible memory for topographical detail runs counter to the general trend of learning experiments with birds (Thorpe, 1951). Matthews (1951*b*, 1953*a*, 1955*b*) has shown that in conditions where Pigeons have only landmarks to guide them, one or two visits to a point are insufficient for a good orientation to result on a subsequent occasion; this was only achieved after six previous visits. He found that Pigeons with experience of flights from up to 110 miles in various directions did not recognize landmarks only 25 miles from home. Even the learning of the immediate surroundings of the loft is slow. Aeroplane observations of Pigeons by Hitchcock (1952) and Griffin (1952*b*) did not give any conclusive evidence as to the importance of landmarks.

Matthews (1952*b*) approached the problem from another direction by training thirty Pigeons to associate food with a white card placed in front of one of a circle of eight pots. Learning was slow, from nineteen to a hundred trials being needed before a run of eight correct choices was obtained. These birds had previously taken part in field tests and their orientation and homing performances calculated. No correlation was found between either of these indices and the rapidity with which a visual 'landmark' was learnt. The birds were tested on the same problem after lapses of 1 and 2 years, giving a retention, measured as percentage saving in trials taken to reach the same level of learning, ranging from 3 to 92 %. Again there was no correlation between the field performances and the excellence of memory for a visual 'landmark'. Excellent visual memory in Pigeons has also been demonstrated by Skinner (1950) after 4 years, and Hardy (1951) lists some apparently well-authenticated cases of Pigeons returning to their loft after 2, 4, 5 and 8 years.

Rüppell (1935) found no difference in homing performance between Starlings released in the migration track and those released in other directions. Griffin (1943) obtained rather better returns with Herring Gulls and Common Terns released in areas that the ringing records suggested would be known to them. However, the differences were not marked enough to be significant statistically. Matthews (1952*a*) also found a similar trend with his gulls, again small. It is probable that as releases in the 'known' area would be on the same coast as the colony, the poorer homers would have a better chance of getting home by searching methods. A number of releases of wild birds a second time at the same place have been reported: one Manx Shearwater (Matthews, 1955*c*), one Lesser Black-backed Gull (Matthews, 1952*a*), eight Herring Gulls (Griffin, 1943), one Sooty Tern, three Noddy Terns (Watson & Lashley, 1915), seven Swifts (Spaepen & Dachy, 1952, 1953), four Swallows (Wojtusiak & Ferens, 1938) and twenty Starlings (Rüppell, 1935). In twenty-two cases the second return was faster, in the other twenty-two slower, or the bird failed to return. Even if the bird always returned faster the second time this would be no proof that visual landmarks were the predominant factor. The exact repetition of some other factor concerned in navigation could produce the same result.

While we can but conclude that random search for known landmarks is completely inadequate as an explanation of homing and migratory flights of the quality that we have been considering, it does not follow that such inefficient methods are never used. Indeed, it is probable that a bird may fall back on them when the primary means of navigation breaks down for reasons that will be discussed later. Also it is possible that some individuals, indeed some species, have no navigational ability and can only employ random search. But in the light of recent evidence this cannot be assumed merely because positive evidence of such ability has not yet been demonstrated in them. Random search may be canalized by the bird interpreting general ecological clues, as suggested by Griffin (1944). These might include the direction of flow of rivers, general vegetation trends, differences in ocean water types, temperature variations and the like. But these suggestions are little more than anthropomorphic guesswork.

We have, however, seen clear evidence of two kinds of navigational ability. First, there is a simple type in which the bird flies only in one particular direction. That directional tendency is either inherited, as in wild birds making their first migration, or learned by experience in racing Pigeons. The flight is terminated in the one case by the cessation of an internal 'drive', in the other by arrival in familiar surroundings. Secondly, we have the type of complete navigation which enables the bird to orientate and fly towards a known goal, no matter in which direction it has been displaced. Again the flight is terminated by arrival in familiar surroundings. The orientation process is innate, but learning is involved in its successful operation and its relation to a particular 'home'.

CHAPTER 5

The Physical Basis of Simple, One-Direction Navigation

THE foregoing parts of this monograph have set out the evidence for the existence of navigational ability in birds. The aim of this and subsequent chapters is to discover what physical features of the environment are concerned in this navigation, and what sensory equipment is needed to react to such stimuli. On the face of it the ability is so extraordinary that the solution of the problem can hardly fail to be extraordinary in itself. All suggestions therefore deserve a close scrutiny before they are rejected.

First then, we will examine the simplest form of navigation: flight in one direction. Middendorf (1855), in proposing the idea of broad-front, one-direction migration also suggested a means of orientation—that birds were capable of detecting the magnetic poles and of maintaining their bearing therefrom. Similar ideas have continued to crop up at intervals, the most recent being that of Allen (1948). An immediate difficulty is the lack of any structure or tissue that could possibly react directly to the magnetic field. Certain forces are indeed produced by placing 'non-magnetic' material in a magnetic field, but they are far too minute to merit serious consideration (Wilkinson, 1949). Rochon-Duvigneaud & Maurain (1923), Griffin (1944, 1952*c*), Henderson (1948) and Wilkinson (1949) all failed to detect any sensitivity to intense magnetic fields (static or moving) in birds. The claims of Barrett (1883) that certain human 'sensitives' could detect magnets by their 'luminosity' should not, perhaps, be taken too seriously, though he carried out an apparently careful series of tests. The direction-tendencies of caged migrants were unaffected by gross distortion of the magnetic field (Kramer, 1949, 1950*a*). Pigeons orientating their flight in the training direction have done so undisturbed by powerful magnets swinging below the head (Matthews, 1951 *b*) or attached to the wings (v. Riper & Kalmbach, 1952). A passing reference may be made to the contention of Cathelin in a long series of papers (e.g. 1935) that birds followed automatically 'les grand courants ariens électro-magnétique', whose existence, let alone the birds' reaction to them, has never been demonstrated.

Martorelli (1899, 1907) suggested that the N.E.–S.W. trend of migration in western Europe was caused by the deflecting action of the Coriolis force on an essentially N.–S. movement. A similar idea was put forward by Geyr von Schweppenburg (1922). They did not propose that the bird should detect and measure the Coriolis force, but that it was deflected passively in the same way as air masses. However, large deflexions occur only when the moving body is free of the earth's surface for a considerable distance, and there would be no appreciable effect on the comparatively short flights of typical migrants. Moreover, Kramer's work has shown that the N.E.–S.W. tendencies are present in the caged migrant, i.e. at the start of the journey. Roberts (1942) and Beecher (1951, 1954) required birds to determine the direction of the earth's rotation, to serve as a compass guide, by actual detection and measurement of the Coriolis force. The extreme improbability of such achievements are discussed later (p. 84). Dubois's (1915) suggestion that the compensatory head movements of a rotated animal are produced by the earth's rotation also, is a physiological improbability and would in any case lead to continuous eastward migration.

A number of authors (e.g. Landsberg, 1948; Suffern, 1949) have considered that regular migrations, particularly those of oceanic species, could be accomplished simply by flying downwind, 'pressure pattern flying' in aeronautical jargon. While there is plenty of evidence that wind plays an important secondary role in migration (p. 5) and in homing (Kramer & Seilkopf, 1950), there is none that it serves as a primary orientation factor. Wind patterns seldom have the required stability, and there is the problem of determining the wind direction in the absence of landmarks. The alternative, that birds are extremely sensitive to pressure changes and so could determine the barometric gradient, and, 'knowing' that winds blow anticlockwise round a low-pressure area in the northern hemisphere, 'ride the isobars', has no factual support.

The idea of the sun acting as a point of reference can be traced back to Schneider (1906), but, rather surprisingly, the idea aroused interest only slowly. Wachs (1926) has only a passing mention of it, though Thomson (1926) appreciated its possibilities, and Rüppell (1944) again inclined to such an explanation. Kramer and his associates have used the technique of studying the directional trends of migratory birds in cages to test this conception of a 'sun-compass'. It was found that satisfactory orientation behaviour could be obtained when the bird, a Starling, was confined in a small drum-shaped cage of 70 cm. diameter placed in a radially symmetrical pavilion of 235 cm. diameter, with its view of the outside restricted to six windows, 26 × 28 cm. (i.e. each subtending an angle of about 18°), equally spaced round the walls. The windows were of such a height as to prevent any view of outside landmarks and the whole pavilion could be rotated at intervals. The directional tendencies of the bird were estimated by an observer lying below and looking up through the bottom of the cage; the general tendency over a short period (10 or 15 seconds) being the basic unit used. Kramer (1950*b*, 1951*a*) found that when the bird was placed in the apparatus with the sky heavily overcast there was no trace of orientation (Fig. 17), but when the cloud dispersed the bird became strongly orientated.[1] Next, mirrors were erected in one of two positions at each of the windows, deflecting the incidence of the sunlight and altering the apparent position of the sun. The direction-tendency of the bird was deflected in the same sense (Fig. 18). Other tests showed orientation, somewhat less precise, under cloud cover of a moderate degree of compactness, or when the light was

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[1] To the north-west and not the normal spring north-east, but as the bird persisted in this direction it was used as a basis for further tests. Throughout Kramer's work few individuals have been used, those which showed themselves amenable to the experimental conditions. This does not detract from the value of his conclusions where they are concerned with *positive* results of experimental treatment.

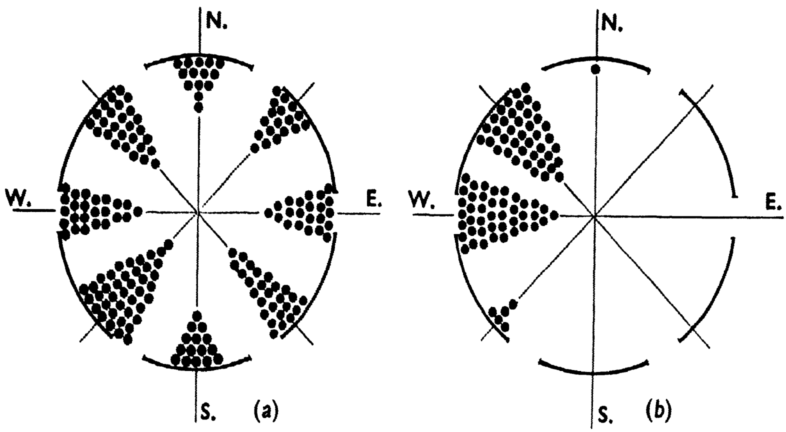

Fig. 17. Orientation activity of a caged Starling at the time of migration. (*a*) Random scatter with overcast skies; (*b*) orientation consistently to W. and N.W. later in day with clear sky. Each dot represents 10 seconds of activity directed to a particular bearing. (From Kramer, 1951*a*.)

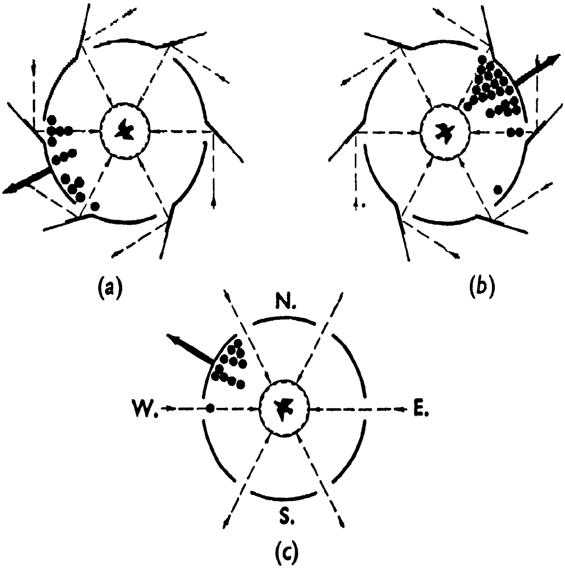

Fig. 18. Orientation activity of a caged Starling at the time of migration. Mirror experiment. In (*a*) and (*b*) mirrors are fixed at different angles at the six windows. This leads to an equivalent change in the direction of activity from that occurring without mirrors in (*c*). (From Kramer, 1951*a*.)

diffused artificially by semi-transparent paper over the windows. However, it was clear that the bird needed to see the general position of the sun, or at least the sky in a rather narrow area around the sun, subtending an angle of 30–45°. It was unable to orientate with reference to a patch of blue sky only, and therefore seems to lack the ability to locate the sun by the associated pattern of polarized light, unlike bees and other arthropods. The mirror experiments were an additional check of this since the polarization pattern was thereby deranged, without affecting orientation. It was further shown that the bird 'preferred' to orientate with reference to deflected sunlight entering one window in competition with direct views of the sky in three or four windows. Montgomery & Heinemann (1952) in laboratory training tests with Pigeons have also failed to demonstrate any special sensitivity to polarized light.

The limitation of these experiments to the periods of migration restlessness was inconvenient, so Kramer & St Paul (1950*a*) now *trained* Starlings to move in one compass direction in the apparatus and take food from the appropriate one of twelve containers arranged in a circle, with precautions against training to 'false' clues. Sun obscuration and mirror tests indicated that this learned orientation had the same basis as the innate orientation, yet could be studied at any time or season. No orientation could be obtained in a closed artificially lit room, confirming the results of Dijkgraaf (1946) who failed to train a Greenfinch, a Siskin and a Starling to move in a particular compass direction. Kramer & St Paul (1950*a*) and Kramer (1952) now trained Starlings to feed in one direction at a particular time of day, and then tested the birds at a different time. The birds still took up the training direction although this now made a different angle with the sun position. The implication was that the birds could make allowance for the regular daily movement of the sun, and that they had some form of 'chronometer' allowing them to measure the passage of time. Indeed, it proved much harder to train a Starling to take up a fixed angle with reference to the sun position, i.e. in a different compass direction at different times of day.

The position was examined further (Kramer, 1952, 1953*c*) by using an artificial sun. This was a 250 watt light source subtending an angle corresponding to that of the sun's disk. It could be raised or lowered vertically and thus set at an altitude corresponding to that of the true sun at a particular time of day. It remained fixed in the horizontal plane. Starlings could be trained to accept the artificial sun in lieu of the true sun and to take up a given direction, say 'west', with reference to it and at particular times. If the bird was now tested at a different time of day it still orientated to the 'west' by making a different angle to the 'sun', i.e. it reacted as if the 'sun' had a diurnal movement. Hoffmann (1953*a*) carried the artificial arrangements further by taking 12-day-old Starlings from the nest-box and rearing them subsequently without any direct view of the sun. Two could be trained to orientate with reference to the artificial sun at a particular time, and one of these showed the progressive changes in direction when tested at other times. This emphasizes the innate nature of the whole process, although there is a slight chance of the birds having seen the sun from their nest-box. Hoffmann (1953*b*) also demonstrated the dependence of the 'chronometer' on the diurnal light/dark cycle. He trained two Starlings in one direction with reference to the natural sun, and then kept them for 12–18 days in an artificial day retarded 6 hours from normal. They were then tested under the natural sun at times when its height was the same as would be 'expected' in the artificial day conditions, 09.00 artificial time and 15.00 normal time. He found that their orientation changed through 90° clockwise from the training direction, as if their chronometers had indeed been retarded by 6 hours (Fig. 19). This new orientation was maintained while the birds were kept under constant light conditions for 23 days. It was then reinforced by training under the retarded day conditions for 29 days. Then after 12–16 days under normal light conditions in an outside aviary the birds were found to have returned to their original orientation, i.e. had regained 6 hours.

These experiments have clearly demonstrated that direction finding, innate or learned, in the Starling is based on the sun. Does this mechanism suffice to explain all one-direction navigation? The fact that migrants continue to pass over in the 'standard' direction when the sky is overcast is no real objection. The direction could well have been determined by an earlier view of the sun and maintained in the cloudy interval with reference to general topography. Analogous perseverance in one direction, but with reference to marks on the inside of the experimental pavilion, was noted by Kramer (1952) when the sun was 'removed'. Tinbergen & Zijlstra (1953) have shown that the direction trends of Starlings and Chaffinches migrating in sunny weather were maintained on a subsequent overcast day but were much more widely scattered on the third morning, which was also overcast.

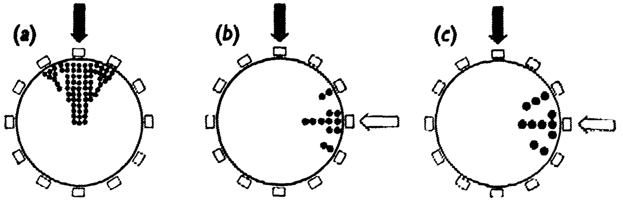

Fig. 19. Changed orientation of a Starling after experimental alteration of its 'chronometer'. The bird was trained to feed from a pot in a fixed compass direction (*a*). After a period in an artificial day 6 hours behind normal time, it chose the pot at 90° from the training direction (*b*). This changed orientation was maintained through a further period of continuous illumination (*c*). Each point represents one choice. (From Hoffmann, 1953*b*.)

It is probable also that night migrants receive their primary direction from the sun. The Starling itself is by no means exclusively a day migrant and, especially later in the season, habitually migrates at night (v. Dobben, 1953). Such typically nocturnal migrants as three Barred Warblers and a Red-backed Shrike have been shown by St Paul (1953) to have a well-developed sun orientation mechanism, by using the same tests with mirrors, time changes and the artificial sun. It would be most unlikely that such an elaborate mechanism would have been evolved and maintained if it were not put to good use. The direction of the night's flight could be determined from the sun during the day, or about sunset, and maintained as well as possible throughout the darkness with reference to topography, and possibly some general guidance from the moon and star pattern. The ready drifting of nocturnal migrants encountering beam winds over the sea (p. 5) and the broad-front nature of their movements (p. 7) fit in with this conception. Kramer (1950*a*) noted that a Blackcap and two Whitethroats showed aberrant directional tendencies when exposed near the sky-glow of a large town after sunset. Placed at the same point *before* sunset the birds showed normal orientation. In the first instance it seems probable that the town lights were taken for the sunset and the birds orientated accordingly.

Orientation with reference to the sun also appears to cover one-directional homing in Pigeons. Schneider (1906) had suggested that the trained birds might fly at a fixed angle to the sun position, being always released in the same direction and at about the same time of day. However, after training in which these two factors, direction and time of release, were kept constant, Matthews (1951 *b*) found that Pigeons would still orientate well in the home/training direction when released 6 hours earlier or later than normal. He also found (1952 *b*) that Pigeons had great difficulty in learning to go at a fixed angle to a crude 'artificial sun' in training experiments under laboratory conditions. This suggested that such a problem was not a 'natural' one for the birds. Finally, Kramer & Reise (1952) trained two Pigeons for direction in a modification of the apparatus used for Starlings, with reference to the natural sun. The Pigeons likewise maintained the direction when tested at different times of the day, and were deflected from it by the arrangement of mirrors.

How then do the birds use the sun as a reference? Kramer and his colleagues have proposed what is at first sight the simplest solution, that the desired direction is determined as a horizontal angle (azimuth), measured around the horizon from the downward projection of the observed sun position to the horizon. This would be reasonable if the downward projection of the sun moved round the horizon at a fixed rate. The bird would then only have to correct its bearing by a constant amount per unit time. But there is in reality no such constancy in the sun's rate of change in azimuth. Consider Fig. 20, which represents the relation between sun and observer in Ptolemaic terms, i.e. the sun moves and not the earth. From this it will be appreciated that the horizontal (azimuth) component of the sun's movement is small early in the day and large around noon.

To take a concrete example let us consider a bird in 51° Lat. (southern England) taking up a particular direction on 22 June. Suppose it does so at 06.00 hours local time, and then 4 hours later at 10.00 hours has to do so again. The original bearing with reference to the sun's position in azimuth will have altered through 53°. To take up the same direction after a further lapse of 4 hours, at 14.00 hours, will require a further alteration not of 53° but of 102°, nearly twice as great. Nor does this diurnal variation in the rate of change of azimuth even remain constant. From its position on 22 June (the summer solstice) the sun's arc sinks below the horizon until an extreme position is reached on 22 December (the winter solstice). This means that the same amount of movement around the sun-arc (change of arc angle, this may be termed) now subtends a smaller angle around the horizon. Thus the bird correcting its bearing between 10.00 and 14.00 hours will now have to make a change of only 56° instead of 102°. The position is further complicated when the bird changes its position, as it does when on migration. In 51° Lat. it

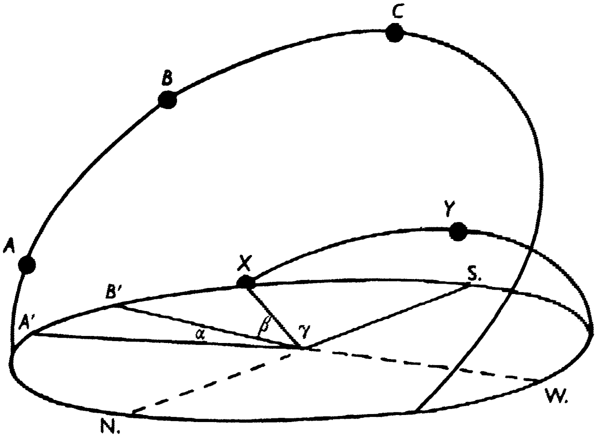

Fig. 20. Perspective diagram of the sun-arc at summer (upper) and winter (lower) solstices for latitude 51°. The sun takes the same time to move from *A* to *B* as from *B* to *C*, but its downward projection moves round the horizon at very different rates from *A'* to *B'* and *B'* to S. Again, *BC* and *XY* are the same length of sun-arc traversed in the same time, but the equivalent movement round the horizon, *B'* to S. and *X* to S. is very different.

has but to move 666 miles west for local time to be an hour behind its home (chronometer) time. If it takes up its selected direction at, say, 13.00 hours by the latter, it will make an error of 28°. A move 691 miles to the south would result in the sun-arc being tilted at a greater angle and lead to an error of 12° at the same time. These errors produced by changes in longitude and latitude would likewise vary according to the time of day and the season of the year. Now, direction-finding with reference to the sun has been demonstrated to be an accurate process which can occur at any time of day and, through the medium of the training experiments, at any time of the year. It is possessed and clearly used by migrants which undergo very considerable displacement. Therefore if we postulate direction-finding with reference to the sun's azimuth position we must credit the birds with possession of the equivalent of a complete nautical almanac, making the necessary corrections automatically. This would seem to be unreasonable, to put it no more strongly. We can believe that a young migrant could inherit the information that it should fly at such-and-such an angle to a fixed reference point. But it is too much to ask that it should fly at one angle at one time, at another angle at another time on the same day, at another angle at the same time on a different day, to change these as it changes its longitude, to change them as it changes its latitude.

And yet there is no doubt that the sun is the essential factor in the orientation mechanism. Moreover, it is capable of providing a *fixed* reference point. The highest point of the sun-arc is always due south in the northern hemisphere. It has been suggested (Matthews, 1951 *a*) that this point could be obtained by extrapolation of the sun's observed path along a part of its arc. This topic is of great importance in connexion with the more advanced form of navigation and will be discussed more fully later (Chapter 9). In the present context the suggestion is that the directionally striving or trained bird is not constantly altering its bearing with reference to the sun's position in azimuth, but is moving at a constant angle to the projection of highest point of the sun-arc. No errors would accrue if the bird did not determine the latter at every observation but simply imposed the remembered characteristics of the arc on the observed sun position. The experimental changes produced by mirrors, artificial sun and chronometer alterations are all accounted for on this basis. Indeed, some puzzling features become clearer. For instance, Kramer (1952, 1953*c*) found that mistakes made under the artificial sun could be largely reduced if care was taken to adjust its height to that appropriate for the time of day. This procedure would facilitate any 'fitting' of an arc by the bird. One Starling first trained under such conditions was later trained to accept the 'sun' at one fixed height. However, this is no more evidence that the altitude is unimportant than is the fact that a direction is taken up at any time of day an argument that the azimuth is unimportant. Indeed, we have seen that another Starling was trained to accept a situation with a fixed azimuth. Then again there is the reorientation of Starlings by chronometer alteration (Fig. 19), where a change of chronometer time of 6 hours brought about a rotation through 90° of the chosen direction. But the azimuth change between 09.00 and 15.00 hours at the season of the experiments (end of April to end of June) is more of the order of 135°. It is the angle the sun traverses along its *arc* that changes 90° in 6 hours. It will be appreciated that at the brief exposure to the natural sun in these experiments the latter would be moving in the contrary direction to that appropriate to the artificial time. But again, the circumstances being familiar to the bird and a speedy choice being required, the fitting of the preconceived arc without attention to the details of the sun's movement would seem plausible.

It would be necessary for Hoffmann's (1953*b*) young sunless Starling to inherit a general knowledge of the sun-arc, but this is already implicit in its clear conception of the movement. He found that his bird 'overestimated' the azimuth change appropriate to the season, mid-October to mid-November. Thus, trained between 15.00 and 16.00 hours and tested between 07.30 and 08.30 hours, the bird was expected to make a change of direction of about 90°, whereas its mean tendency exceeded this by 43°. Hoffmann sought to explain this by suggesting that the bird was using the rate of change in azimuth appropriate to June, when the bird had been in the nest. But as it was not supposed to have seen the sun this does not seem very plausible.

Now if the bird was concerned with the sun's movement along its arc, the time change would result in a change in 'arc angle' of 112°. This fits the results better and brings the Starling's 'error' within the limits likely to be expected in such very artificial conditions. Kramer (1953*c*) records results with another Starling under the artificial sun in October which also made 'mistakes' that usually involved it in making a bigger angle than the experimenter expected (Fig. 21). Yet another bird tested in August (where the azimuth change is large) made fewer 'mistakes', mainly 'underestimates'. While it would be unwise to build too much on the results obtained with so few birds it is at least clear that these observations are capable of an interpretation other than that which has been placed on them by Kramer and his colleagues.

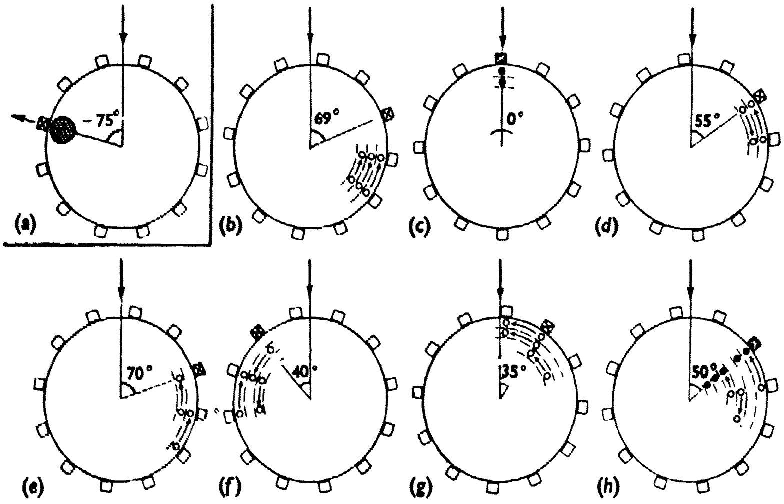

Fig. 21. Changed orientation of a Starling with reference to a fixed artificial sun according to the time of day. The bird was trained to feed from a pot in a fixed direction at a fixed time of day (*a*). Tested subsequently at different times of day (*b*–*h*), it changed its orientation with reference to the 'sun' as if the latter had moved. The pot it was expected to select is marked with a cross. (After Kramer, 1953*c*.)

The form of one-direction, coastward orientation shown by Common Terns (p. 18) was also dependent on the sun.

CHAPTER 6

Theories of Complete Navigation by the Maintenance of Sensory Contact with Home

ATTEMPTS to account for the second, complete form of bird navigation had given rise to a multitude of theories long before it was conclusively shown that such navigation existed. The theories fall into two mutually exclusive groups, those which suggest that the bird maintains a sensory contact with home, and those which require it to react to quantitative differences between stimuli present at release and at home. The latter will be discussed in later chapters, here we will examine theories whereby the bird continues to perceive its home directly, and those whereby some feature of the surroundings is recognized as the last link in a series of such features, a thread of Ariadne, leading back to home.

Direct visual perception over immense distances was postulated by Hachet-Souplet (1901, 1909, 1911) after he had demonstrated the importance of vision in Homing Pigeons. Although birds' eyes are undoubtedly superior to our own in many respects (Chapter 9) it is very doubtful whether their range of vision exceeds ours. In any case a definite limit is imposed by the curvature of the earth, the distance of the horizon in miles being $1{\cdot}32\sqrt{h}$, where h is the observer's height in feet. Migrating birds seldom fly above 3000 feet (horizon 73 miles) and frequently much lower, as has been demonstrated by observation both from the air (e.g. Meinertzhagen, 1920; Grashof, 1936) and from the ground (e.g. Deelder & Tinbergen, 1947). Pigeons, gulls and shearwaters have been observed to pick up their homeward orientation when flying low, as a general rule at 200 feet (horizon 19 miles) or less. The presence of high mountains and of cloud formations over isolated islands and along coast-lines would, of course, increase the effective range of vision, though cloud formations would not be characteristic of any *particular* island or coast. Contrariwise, the atmosphere conditions will seldom allow the theoretical range of vision to be achieved. Duchâtel (1901) postulated a sensitivity to infra-red rays which penetrate haze. Wojtusiak (1949) even suggested that by such means birds could navigate visually at night, perceiving the warmer southern regions. Vanderplank (1934) claimed to have demonstrated a visual sensitivity to infra-red rays in owls, but this was denied by Matthews & Matthews (1939) and Hecht & Pirenne (1940) for owls, and by Watson (1915) and Lashley (1916) for chickens. From a purely logical viewpoint it is unlikely, as Pirenne (1948) has pointed out, that an eye which is itself producing quantities of infra-red radiation would be sensitive to such rays. He draws the analogy of a red hot camera taking a picture of a red hot poker.

A special sensitivity to the physical and chemical constituents of the atmosphere as a means of distant detection of the home area has been frequently suggested since the time of Evans (1795). It is generally looked upon as an extra sense not necessarily allied to that of smell. Various parts of the body have been proposed as its site, such as the air sacs by Fatio (1884, 1905). But Hachet-Souplet (1911) and v. Oordt & Bols (1929) found that Pigeons homed successfully with these structures collapsed by puncture. Cyon (1900) suggested the nasal cavities, but his own experiments were unconvincing and Watson & Lashley (1915) found the homing of Noddy Terns unimpaired when the cavities were blocked with wax. Recently Anon. (1949) sought to endow those uniquely avian structures, the feathers, with such properties, a theory quite safe from experimental investigation.

Odd theories calling for 'radiations' of an unspecified nature from the home area frequently crop up in popular literature. Mattingley's (1946) contribution served its purpose by calling forth a devastating counterblast from Thomson (1947). The parapsychologists Rhine (1951) and Pratt (1953) have suggested that some extra-sensory means of orientation is the basis of homing. However, even if we could accept their findings as to the reality of telepathy, clairvoyance and psychokinesis in Man (and Spencer-Brown (1953) has made a sharp attack on the logical and statistical nature of their evidence), it is difficult to see how such phenomena, if they existed in animals, could be of assistance in homing. Their independence of ordinary considerations of time and space has been strongly emphasized by their advocates, so they could hardly be of use for two-dimensional orientation. Indeed, no suggestions as to the mode of operation have been forthcoming from the parapsychologists, who really became interested in bird navigation only because the known facts had then received no adequate explanation in terms of sensory physiology. We may also mention here, and dismiss, vague theories of a special 'sense of space' which means nothing and explains less. Katz (1937) made an interesting attempt to resolve the problem on psychological lines, but really got no further than an appreciation of the intense awareness of the orientation of *familiar* surroundings that we ourselves have.

Let us now turn to the retracement theories and see what substitutes for Theseus' guiding thread have been proposed. A succession of visual landmarks does not excite wonder and it is highly probable that proximate orientation, the final pinpointing of the home, is brought about in this way. But this succession could not be extended indefinitely even when the outward journey is made by the bird as a free agent. We have seen (p. 56) that Pigeons are slow to learn visual landmarks in the laboratory or in the field. And, of course, in the great majority of homing experiments precautions have been taken to prevent the birds seeing anything of their surroundings while being transported to the release point. Wallace (1873), concerning himself mainly with the homing of mammals, suggested the use of odour memories. Bennett (1873), clearly an early 'experimental biologist', proposed to mask the external odours by hanging some stale fish in the animal's travelling box. Despite a good deal of controversy it would seem that most birds have a very poor sense of smell, witness the reflexological work of Walter (1943) for instance, and this possible guidance would be denied them in any case.[1] Moreover, this theory would require a slavish retracing of the outward path and so be subject to easy check. Jebb (1873) actually took his dog along two sides of a triangle and found it returned home so quickly that it must have completed the third side (10 miles).

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[1] In members of the Tubinares (Albatrosses, Shearwaters and Petrels) the olfactory organs and the corresponding part of the brain are quite well developed (Wood Jones, 1937). It is possible that the proximate orientation of those species which only visit their nesting burrows at night may be assisted by olfactory clues. Certainly their eye structure is not adapted for

We come next to the retracement theory that requires an animal to remember the outward route through space by registering all the twists and turns to which it was subjected in its box. This suggestion is usually attributed to Reynaud (1898) with his 'loi de contrepieds' and to Bonnier (1903). But Spalding (1873) and Darwin (1873) both had this conception in general terms, and Murphy (1873) put forward a plausible mechanical analogy, an early 'biological model'. This was a ball freely suspended from the roof of a railway carriage, reacting to shocks given to it by changes in the latter's direction and velocity. He conceived that '...a machine could be constructed in connexion with a chronometer, for registering the magnitude and direction of all these shocks, with the time at which each occurred; and from these data...the position of the carriage, expressed in terms of distance and direction, might be calculated at any moment....Further it is possible to conceive the apparatus as so integrating its results...that they can be read off, without any calculation being needed.' Without this conception of constant integration the whole hypothesis would quickly be reduced to absurdity since the most exact retracement of the outward path would be required. Detour experiments such as that of Jebb, and, with Pigeons, of Hachet-Souplet (1911) and Matthews (1951 *b*) effectively dispose of any lingering doubt on this point. The idea of an animal performing a mental triangulation is no longer so bizarre since v. Frisch (1950) has clearly demonstrated that bees can do this.

Exner (1893) suggested that the semicircular canals of the inner ear would provide the type of mechanism required to subserve this 'sense'. Meise (1933) added the hypothesis of

night vision (Lockie, 1952), and the mate need not be present to assist by calling. Even to the insensitive human nose the body odour of these birds is most marked and very distinct from that of the Alcidae or Pelicaniformes, and distinguishable down to generic level at least in the Procellaridae themselves. Detection of individual differences in body, and hence burrow odour by the birds would thus not seem impossible.

'muscle memories', or proprioceptive recordings, in those cases where the outward journey was effected by the animal itself. He was then visualizing an extension of the kinaesthetic learning which plays some part (Munn, 1950) in maze learning by rats. The proposal is of dubious merit and, in any case, applicable to none of the experimental homing tests. The theory would have to rest, therefore, on labyrinthine recording. On the face of it the whole idea seems quite impossible—that the available apparatus could detect and record every change of direction and acceleration against a background of much greater jolts and jars from the transporting vehicle. It would be rash to assert that the bird's apparatus would be as ineffective as the human counterpart certainly would be, for there is little to be gained by argument as to the limits of efficiency of biological systems when we are unsure of the initial assumptions that must be made. Direct experiment is much more satisfactory.

Observation shows that birds are often asleep during transportation, and it must therefore be assumed that the recording process would have to function during unconciousness. This further reduces its plausibility. Confirmation comes from experiments in which birds have been transported under heavy anaesthesia—Pigeons by Exner (1893), Starlings by Kluijver (1935) and Herring Gulls by Griffin (1943). In no case was the homing result poorer than that with untreated birds in comparable circumstances. Another approach is to make the outward journey so complicated that it would be beyond reason for any recording apparatus to cope with it. Rüppell (1936) using Starlings, and Griffin (1940) using Leach's Petrels rotated their birds on turntables and reported no deleterious effect on homing. However, rotation was limited to part of the journey and/or the releases were not sufficiently far from known territory to make returns by random searching improbable. Matthews (1951 *b*) therefore carried out a series of tests with Pigeons taken to the release point in a large light-proof drum turning horizontally at about four revolutions per minute. The construction was unstable so that changes in the speed and direction of the transporting vehicle produced a momentary slowing of the drum. The outward journey through space was thus remarkably complicated by the irregularly varying rotation, about 1200 revolutions in the longest journey. Nevertheless, in every case the performance of the rotated birds, both in orientation and returns, was just as good as the untreated controls.

Of course a devoted supporter of the hypothesis would still be able to say that the mechanism was so perfect that it could cope with such a complicated system. A final answer would be obtained with the destruction of the labyrinth itself, though such operative treatment is undesirable because of the widespread effects it would have, and only negative results would be acceptable. Normal homing by Pigeons has in fact been reported after blocking of the auditory canals (Casamajor, 1927; Grundlach, 1932); destruction of the tympanic membranes (Hachet-Souplet, 1911); extirpation or cutting of the horizontal semicircular canals (Hachet-Souplet, 1911; Sobol, 1930; Huizinger, 1935); and removal of the pars inferior and both after ampullae (Huizinger, 1935). The distances involved in tests after recovery from the operation were often not as great as could be desired, though Hachet-Souplet reported good returns from up to 240 miles. But the weight of negative evidence is impressive. Casamajor (1927) reported impairment of homing after injection of quinine chlorohydrate which, in humans, produces buzzing noises in the ear, and Treat (1947) after decompression to an indicated altitude of 25,000 feet. Both treatments, however, could well have had generally deleterious effects.

We may conclude that it is highly improbable that recording and integration of displacements experienced during the outward journey could act as a basis for bird navigation. Before leaving the ear-apparatus, mention may be made of one more curious hypothesis. In a series of papers Vitali (e.g. 1912) described a small innervated vesicle, the para-tympanic organ, in the middle ear. Neither he nor anyone else has been able to assign any sensory function to this organ. A few centuries earlier it would no doubt have been described as the 'seat of the soul'. Vitali believed that it was the site of the 'homing sense'. Benjamins (1926) showed that cauterization of the organ in both ears had no effect on the homing of Pigeons.

Having severally disposed of the theories in this group we may consider an objection that rules it out as a whole. A recurrent feature of homing experiments carried out by a number of workers was that birds released quite close to home were taking very much longer to return, proportionately, than those released at greater distances. Griffin (1943) sought to explain this by suggesting a reluctance to return to the home area when the unpleasant memories of trapping and handling there and at release were associated and strengthened by proximity. But Matthews (1952*a*) showed that Lesser Black-backed Gulls released a quarter of a mile from the colony returned to their nests in a few minutes, pausing only for a preen and bathe. Nor could Griffin's explanation apply in the case of tame Homing Pigeons where the same effect had been noticed. However, in this case the short distance releases were generally of young birds and their hesitation could be attributed to their lack of experience of homing and, perhaps, to their treating the release as a normal daily exercise flight. On the other hand pigeon-fanciers would assert that even old birds clear away from the release point more quickly at greater distances. But the circumstances of pigeon-races made such information difficult to evaluate. To test whether there was a real 'distance effect' Matthews (1955*b*) used two teams of experienced Pigeons that had survived a series of experimental tests, each individual having an already extensive history of single releases up to 110 miles from home in most directions. Their orientation in the last tests in which they took part is shown in Fig. 22*a*, giving a good homeward orientation with an average deviation of 39°. Yet when these same birds were released, in good, sunny conditions at points not previously used only 25 miles from home they showed no signs of orientation at all (Fig. 22*b*), average deviation 85°. Released closer to home, at 10 miles, a coarse orientation (47°) resulted which could be clearly attributed to memory of landmarks since it became generally better at closer distances still, though with variations, as if some release points had been flown over more frequently than others. Taken 35 miles to another point the birds again gave a near random scatter, associated as in the other non-orientated releases with slow returns. At 50 miles good orientation has been achieved by these and many other Pigeons.

Thus instead of the means of distance orientation becoming more and more effective as home is approached, as we would expect from systems discussed in this chapter, it appears only to come into operation somewhere between 35 and 50 miles from home. Somewhere between 25 and 10 miles from home these particular birds were able to pick up their orientation from remembered landmarks. This limit would naturally vary with different birds, their experience and the topography of the surrounding country. In between there would seem to be a ring of country in which the birds would have no means of direct orientation, and presumably have to fall back on random search methods. As we have seen from our discussion of Wilkinson's work (p. 33) this is an effective process when short distances are involved. Beyond 50 miles there is suggestive evidence that the accuracy of orientation increases with distance, though this is not so firmly established as yet. The result of this work, showing a marked 'distance effect' and a necessary minimum displacement for the operation of the navigational system is much more in accord with the requirements of the second group of theories, involving quantitative comparison of stimuli, which we will now consider.

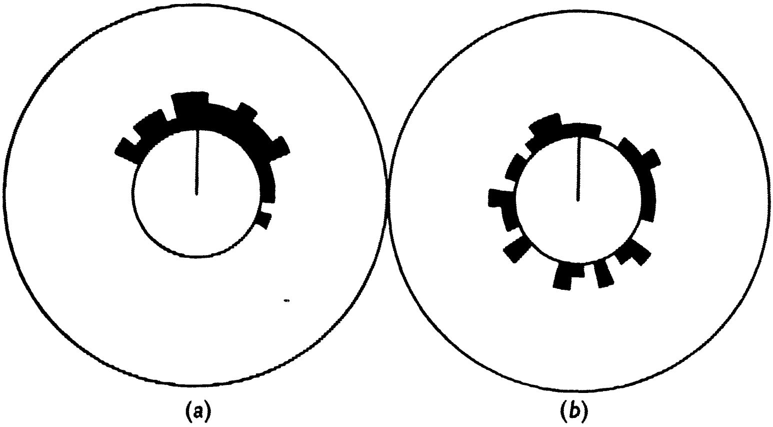

Fig. 22. The 'distance effect' in the orientation of Pigeons. (*a*) Pigeons released at unknown points in sunny conditions 60–110 miles from home gave a good homeward orientation. (*b*) The *same* birds subsequently released in similar conditions but only 25 miles from home gave a random scatter.

CHAPTER 7

Theories of Complete Navigation by means of a 'Grid' Derived from the Earth's Rotation and Magnetism

LET us suppose that there is some physical factor, X, that varies quantitatively in a regular way across the earth's surface. Let Y be another factor with a gradient at an angle to that of X. Then the isolines joining places with equal values of X will cross the isolines of Y to form a 'grid' as in Fig. 23. In a perfect 'grid', in which a given isoline of X crosses a given isoline of Y only once, any point will be uniquely characterized in terms of X and Y. Thus, in the figure, the home has a value of $X_{10}Y_8$ and the release point of X_2Y_3. Clearly the greater the angle at which the isolines intersect the more precisely will a given pair of values characterize a given point—in navigational jargon, the better will be the 'fix'.

The simplest way in which such a 'grid' could be used would be for the birds to show a form of *kinesis*; that is, to move off at random, but then tend to fly more in those directions which resulted in X and Y approximating more closely to the remembered values at home, and, conversely, to fly less in those directions which increased the differences. Such biased wanderings would eventually result in the bird arriving near the home point. It would further be reasonable to assume a complete bias, that once the bird had determined the lie of the gradients it would fly along the resultant towards home. But if the birds undertook such initial sampling movements they would be expected to leave the release point in any direction, whereas we have seen that a definite homeward orientation is observed. This would only be achieved in a sampling process if the bird was able to detect and measure the gradients while it was within a mile of release. An accuracy of this order is extremely unlikely for any of the possible physical bases of such a 'grid', especially as a much greater sensitiveness is required to detect a slow continuous change than to detect the difference between two discontinuous values.

Such a comparison of home and release point values would become easier the farther apart the two points were and, conversely, would require a certain minimum displacement—the 'distance effect' which we have demonstrated in the Pigeon.

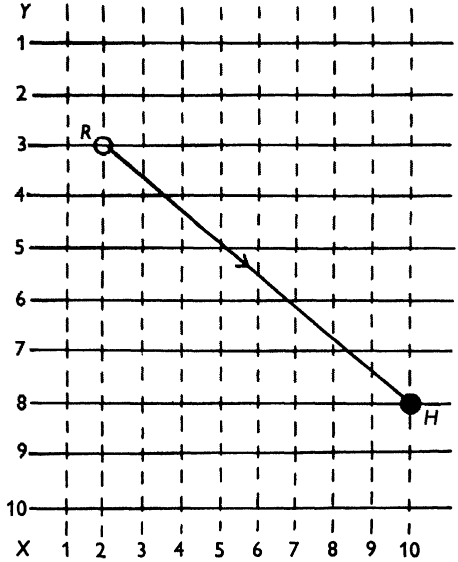

Fig. 23. Diagram of a 'perfect' navigational grid. Two physical factors, *X* and *Y*, vary in a constant, quantitative fashion across the earth's surface, with their gradients at right angles to one another.

But another element in the navigational system is required if, after such a comparison, the bird is to leave in the direction of home shortly after release. It must 'know' that if factor *X* is less it has to move in one direction across the grid, if it is more, in the opposite direction; and similarly with factor *Y*. Further, to translate this into practical flying, it must be able to determine the orientation of the *grid* with reference to the surroundings of the release point, much as we 'set' a map by coinciding its northing line with the compass needle.

Ising (1945) made a detailed analysis of the various dynamic consequences of the earth's rotation, and the ways in which they could be used by a bird for navigational purposes. Thorpe & Wilkinson (1946), de Vries (1948) and Wilkinson (1949) made calculations to relate Ising's proposals to the potentialities of the sense organs likely to be concerned. A basic weakness of Ising's suggestions is that the effects he considers could at most provide only one set of isolines, corresponding to the parallels of latitude, not a complete navigational grid. First, then, we have centrifugal effects. As a body moves towards the equator, the sideways force is increased, tending to offset the downwards force of gravity. As a result the body apparently loses weight. But for a displacement over 50 miles the change is very slight, of the order of one part in twenty thousand, say 0·02 gm. in a Pigeon. This is far less than changes produced by metabolic processes that would be going on during the journey to the release point. Also weight-changes some ten times greater are produced when a bird which has been flying east, adding its speed to that of the earth's rotation, turns and flies west.

A second effect of the earth's rotation is the production of the so-called Coriolis force. Its nature is best illustrated by Wilkinson's model of a particle situated on the edge of a disk of radius r. If the disk is rotating about its vertical axis with an angular velocity w, the particle's sideways velocity will be rw. If the particle moves towards the axis, say half-way along the radius, its sideways velocity is now $rw/2$. By definition, such a diminution of velocity must have been produced by a sideways force acting in the opposite direction. This is the Coriolis force, of magnitude $2mwv'$, where m is the mass and v' is the velocity with which the particle moves towards the axis. If we imagine the earth's sphere to be made up of a series of concentric disks of diminishing radius, a body moving north over the surface is effectively moving towards the axis as it passes from the edge of one disk to that of another. The rate at which it does so is a function of the bird's velocity v, and the latitude λ, $v' = v \sin \lambda$, giving the Coriolis force as $2mwv \sin \lambda$. Again if the bird was not moving due north the angle of deviation would affect the result, though theoretically the latitudinal and directional components could be disentangled. Detection of the Coriolis force could be by one of two methods. The first is that of Yeagley (1947) who suggested it could be detected directly as a sideways force on the flying bird. But this would require the bird to estimate (or hold constant) its ground speed to within 0·2 m.p.h., which would be a most remarkable achievement. Similarly its mass must be estimated or held constant to within 2 gm., which would be difficult because of metabolic changes and such incidentals as defaecation. In the unlikely event of these requirements being met the bird would still have to measure a sideways force of less than 1/6000th that of gravity, from which it is only distinguished by its direction of action, i.e. gravity would now seem to act at a small angle to its normal direction. This angle would have to be measured to within 0·2″ of arc—an implausible feat rendered impossible by the fact that, since gravity is already supplying the direction of the resultant force, the bird has no other vertical reference from which to measure the angle. Further, any incidental accelerations such as those caused by wind gusts would produce centrifugal forces indistinguishable from and greatly exceeding the Coriolis force. Indeed, any measurement of the latter by a *flying* bird is out of the question unless it is flying a perfect course and its instantaneous rotation is that of the earth. A deviation of the order of one inch in a mile, in vertical or horizontal planes, would produce spurious Coriolis forces that would mask those due to the earth's rotation. This would seem to be an impossible requirement even though, as we shall see later (p. 109) a bird's *head* is remarkably stable in flight.

The second method of detecting Coriolis force, that originally suggested by Ising, is both more subtle and more feasible since it can be used by a bird at rest and, further, no measure of its total mass is necessary. He considered the effect of the Coriolis force on fluid contained in a ring-shaped tube, and thus of constant mass. If such a tube is held horizontally and then tilted at some constant rate about its east–west axis, the fluid in the northern half of the ring moves towards the earth's axis, that in the southern half away from it. The fluid in each half thus experiences an equal Coriolis force but in a different direction. If the fluid was already flowing round the ring, the result will be a couple tending to turn the ring, analogous to the effect of a magnetic field on a wire loop through which flows an electric current. Ising was able to demonstrate such a rotation in a glass model 20 cm. in diameter and with a rate of flow of 30 cm./sec. But the only tubes in an animal with a liquid flowing rapidly through them are the arteries. These are subject to intermittent pressure fluctuations very much greater than the minute lateral pressure the couple would produce.

A second effect of tilting the ring, and the resultant Coriolis forces, would be a streaming of the fluid round the ring. There would then be no requirement for a prior movement of the contained fluid, and the semicircular canals of the inner ear would be suitable structures for the detection and measurement of the force by this method. On such a scale the amount of energy produced is very small. Ising calculated that for a ring 1 cm. in diameter and 1 $mm.^2$ cross-section, containing fluid of density 1 and viscosity zero, it will, on turning through about 6°, gain a maximum Coriolis energy of 2×10^{-13} ergs. This is only ten times the Brownian agitation energy present in the detecting structure. Moreover, the extra energy is in the liquid and has to be transferred to the detecting sensory hair, or whatever it be, with a considerable loss of energy. This reduced energy would have to be measured to within 10^{-15} ergs to be of use in latitudinal determination, and against a background of the swirling caused by rotation of the ring at right angles to its diameter in its accepted function of analysing postural changes. Thorpe & Wilkinson (1946) showed that there is no tendency for the semicircular canals of long distance migrants and proven homers to be larger, relatively or absolutely. Indeed, the diameter is often only half that of Ising's example, with a hundredfold reduction in the energy produced, requiring measurement to within less than 1/1000 of the masking Brownian energy.

The theoretical approach is so damning that we may consider that determination of latitude or direction from the Coriolis force due to the earth's rotation to be quite impossible on the biological scale. There has been no experimental check on this conclusion. If birds, kept in constant but irregular motion right up to the moment of release were able to orientate when in flight, the case against the hypothesis would be even more definite. It may be a little naïve to add that Pigeons are *not* to be seen shaking their heads in their baskets prior to release.

Hypotheses that the earth's magnetic field could provide a navigational grid date back to Viguier (1882). He suggested that birds could detect and measure the three components of the field, its intensity, inclination (the angle which a compass needle makes with the horizontal) and declination (the angle between magnetic and geographical north). These vary more or less independently of each other so that their isolines would form a complex grid. This hypothesis has been restated, with minor variations, by Thauziés (1898, 1910) Stresemann (1935) and Daanje (1936, 1941). The complete lack of evidence for any direct reaction to a magnetic field in birds has already been discussed (p. 59). Further, Casamajor (1927) and Wodzicki *et al.* (1939) found that fixing magnets to the head of the Pigeon and the Stork, had no effect on their homing ability. Rochon-Duvigneaud & Maurain (1923) pointed out other theoretical difficulties. An important one is that measurement of declination requires an exact knowledge of geographical north. We shall see (p. 68) that the south point may be determined from observation of the sun-arc, but such a difficult feat could hardly be equated with another based on an entirely different 'sense'. Elimination of the declination isolines from the magnetic grid reduces the plausibility of the whole scheme, since the inclination and intensity isolines generally cross one another at oblique angles, making good 'fixes' impossible.

The original concept of a direct sensitivity was therefore replaced by one of indirect sensitivity to the earth's field, and the whole hypothesis was resurrected by Yeagley (1947). He suggested that the earth's field could be detected by the flying bird acting as a linear conductor moving through the lines of force of the field. Theoretically this would result in a small potential difference being set up between the two ends of the conductor, though this has not been demonstrated in practice. Even in theory the induced voltage would be exceedingly small, and would require measurement to within one millionth of a volt if it was to be used for navigational purposes. Further, the bird would be required to make an accurate estimate of its ground speed, to within 0·2 m.p.h. An even more cogent objection was raised by Davis (1948), Slepian (1948), Varian (1948) and Wilkinson (1949) who indicated that the minute voltages would have to be measured against a background of the far more powerful electrostatic field of the earth, about one volt, and of the fluctuating effects of charged clouds. Wilkinson pointed out that a more satisfactory method of detection would be a conducting loop (such as a semicircular canal) oscillated in the earth's field. On the dynamo principle an alternating current would be induced which is much easier to measure than a potential difference. Also the necessity of knowing the ground speed would be avoided. But again the effect is minute and the current would have to be measured to within a thousand-millionth part of an ampere. And once again there would be much more powerful background effects, in this case the physiological currents.

While the theoretical case against the detection and measurement of the earth's magnetic field by indirect methods is overwhelming, a good deal has also been done to test the hypothesis from a practical point of view. When dealing with biological systems the results of such experiments are always more convincing than physical arguments that may be based on false premises. Techniques aimed at disturbing an electro-magnetic apparatus had been reported by Exner (1893) and Griffin (1940). The former passed electric currents through the heads of Pigeons before release, while the latter subjected Leach's Petrels to an intense electro-magnetic field for a few seconds before the beginning of the outward journey from home. In both cases no effects on homing were apparent, but the techniques were not very critical as it is really required that the bird should be subjected to 'interference' during the actual flight. Fixing magnets rigidly to the head will not be a satisfactory test since the additional field would be a constant which could be taken in to account by the analysing mechanism. It is therefore essential that the magnets should move relative to the bird's body. Yeagley (1947) attached small, powerful magnets to the wings of Pigeons, sewing them on through the metacarpal joints. The fluctuating e.m.f. induced in the bird's body when the wings were beating would swamp any measurement of that induced by the movement of the body through the earth's field. Using only ten Pigeons treated in this way and ten control birds with copper bars, Yeagley claimed to have established that the magnets had a strongly deleterious effect on homing. But the difference in performance was not statistically significant and the loss of several magnets in flight suggested that they may have been attached unskilfully whereas the control bars were attached by one used to the work. A similar test carried out by Yeagley in 1945, which gave completely negative results, found no mention in his 1947 paper. It was admitted only much later (Yeagley, 1951), upon a plea that there was abnormal sunspot activity on the day in question. In the meantime Gordon (1948) repeated the test with more adequate numbers and a negative result. Unfortunately, it was later found that at least some of his Pigeons had flown over the test course previously, thereby throwing doubt on the results. Matthews (1951 *b*) carried out further tests with wing magnets under satisfactorily critical conditions and found that they had no effect on initial orientation or on speed of return. Schumacher (1949) suggested that there might be receptors in the wings themselves, cutting the lines of force as they beat. The attachment of magnets to the wings would not then be critical. This is an implausible point but is answered by those experiments in which the magnets were attached to the heads of birds, and other tests by Matthews (1951 *b*) in which larger and more powerful magnets were suspended from neck halters so that they oscillated freely in flight. Again the results were entirely negative.

On the basis of his first and quite inadequate experiment Yeagley proceeded to develop and test his hypothesis on a grand scale. The modified hypothesis of magnetic navigation would provide only one set of isolines, one co-ordinate of a grid. To provide the other set, Yeagley proposed that birds were also able to detect and measure the Coriolis force due to the earth's rotation. We have already seen that this is impossible, and a theory which requires the evolution of two special 'senses', otherwise useless to the animal, is immediately suspect. Yeagley pointed out that since the two systems were based respectively on the magnetic and geographical poles, a given magnetic isoline would cross the same Coriolis isoline at least twice, producing two 'conjugate' points indistinguishable from each other by a bird using the proposed type of navigation. If Pigeons trained to home to one conjugate point were released near the other, they should home to the latter. Yeagley tested this conception with remarkable prodigality, using some 1200 Pigeons. These were trained to a special mobile loft in Pennsylvania, a large structure having 'a peak resembling a church spire and the whole painted a brilliant yellow'. In addition a 5-foot balloon was flown 150 feet above. To ensure that the birds would home to the loft in different surroundings, the structure was moved bodily every day, over several miles. When training was complete the entire set-up was transported 1400 miles to the conjugate point in Nebraska. It is difficult to ascertain what happened then, for as Thorpe (1949) remarks, 'Yeagley's [1947] paper is so constructed that information on many essential points is either lacking altogether, or at best can only be extracted by considerable labour combined with the study of large-scale maps. . . '. This stricture applies equally to the later (1951) paper. In a number of cases at least the birds were allowed to fly freely around the new loft site. They were then released, usually at distances of 50–80 miles, somtimes as little as 25 miles, in small groups. From 459 Pigeons so released when one or two lofts were in position near the conjugate point, *only eight regained a loft.* Five of these were from a single release and could well have remained together. This feeble result was less than one would expect on a random radial scatter, and much less than would be achieved by the type of random exploration discussed in Chapter 3. Unfortunately, no ground observations seem to have been made of the initial direction taken by the birds. In a final experiment ten groups of Pigeons were followed by a light aircraft for more than 25 miles from the release point east of the conjugate point, and these did show a westerly trend. But no emphasis can be laid on one isolated result until confirmed by releases from other directions.

The bulk of Yeagley's analysis depends on reports of the positions at which Pigeons were subsequently recovered, both in experiments with the loft(s) present and in others where the birds were simply launched into the void of Nebraska. The line from release to recovery point was termed the 'flight line', an unfortunate term since the recovery was often made many days later and the bird certainly did not fly straight to the recovery point. Even more misleading was Yeagley's method of analysis.

He split the 'flight lines' into two components, X according as to whether they were towards or away from the conjugate point, Y according as to whether they were to the left or right of the line joining release and conjugate points. He then summed these components algebraically to obtain an 'average flight vector'. This procedure is absurd. For instance, if 360 birds gave 'flight lines' of equal length, spaced at 1° intervals round the compass rose, then the 'average flight vector' would be nil. If one more bird was released its 'flight line' would become the 'average flight vector' for the whole 361 birds. Again, the 'average flight vector' might point in a direction in which no birds flew, as when two 'flight lines' diverged at a wide angle.

A more reasonable approach would be to determine whether the 'flight lines' showed any significant tendency to concentrate about the bearing of the conjugate point, to determine their average deviation. Griffin (1952*c*) calculates that the data in Yeagley's 1947 paper give an average deviation of 64°, which is hardly impressive (illustrations of these scatters are given in Kramer (1948) and Matthews (1951*a*)). For his 1951 paper the value is 80°, and Fig. 24 shows clearly the essentially random scatter of recovery points. In fact it is found that there is a rather less deviation (73°) from the true home direction. Clearly no emphasis can be laid on such slight tendencies until the possible effects of other factors have been analysed in detail. In particular, the less dense human population to the west and north; the publicity given to the experiments in local newspapers and by setting up a loft in the local fairground; the increasing hilliness to the west (the birds' home country is hilly); the winds on the days following release. The data in Yeagley's papers are insufficient for any assessment to be made, the lack of precise information on winds being particularly regrettable. In the first experiment winds of force 4–9 are mentioned and could not fail to have some effect. Odum (1948) gives instances, from a general study of weather maps, in which results could be interpreted in terms of wind drift.

Even the deviation analysis gives equal credit to a gross 'overshoot' and to a recovery in the target area. There should be a demonstrable tendency for the recoveries to be closer to the conjugate point than when they were released. Considering all

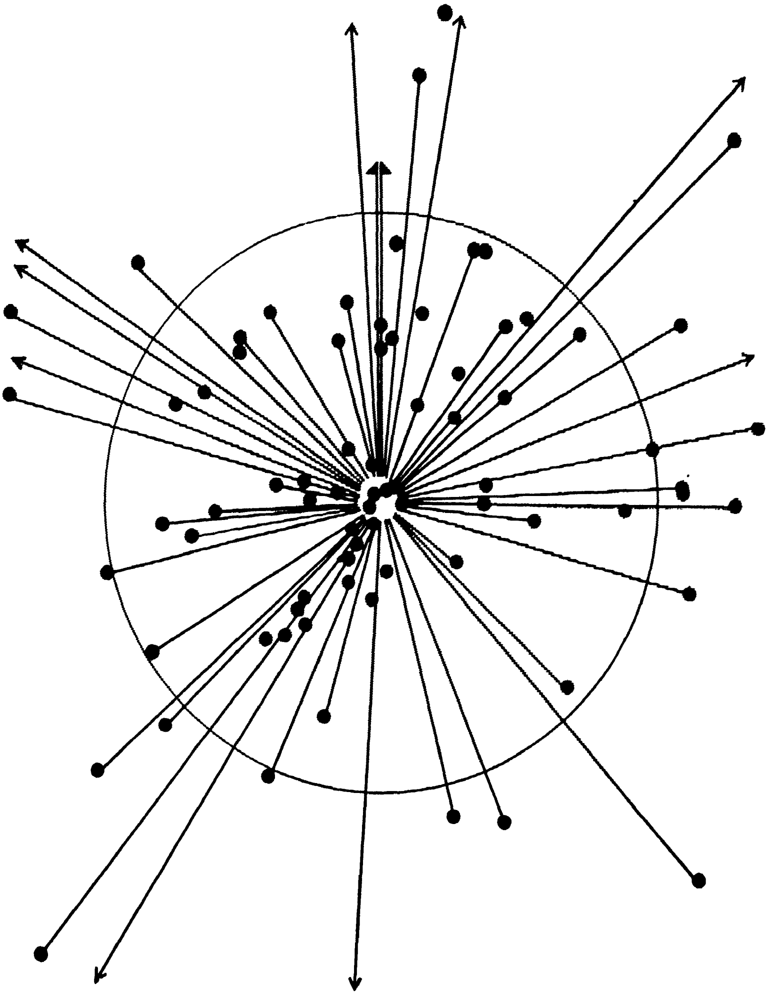

Fig. 24. Subsequent recoveries of Pigeons released near the magnetic/Coriolis 'conjugate point' in Nebraska. The results for eight experiments coincided about one conjugate point bearing, represented by the large vertical arrow whose head terminates on the most distant position of the conjugate point from the release point. Radiating lines terminating in arrows refer to recoveries outside the limits of the diagram. The circle has a radius of 100 miles. (Constructed from data in Yeagley, 1951.)

the 175 recoveries of trained birds released in Nebraska which did not remain at the release point, we find that on the average they were released 70 miles from the conjugate point, and travelled 100 miles to the recovery points. But these averaged 105 miles from the conjugate point. In short, the birds were farther from their 'aiming point' than when they were released, half as far again in fact.

Yeagley's hypothesis is therefore completely unacceptable not only because of its theoretical 'impossibility', but also because the massive field experiments have produced entirely negative results. An obvious omission was any attempt at control releases in some place *not* near a conjugate point, to check on the type of distribution obtained in Nebraska. The more or less random scatter of the recoveries is a surprising feature, since with such a gross displacement it would be expected that a grid navigation, whatever its nature, would give a firm homeward orientation. Possibly the technique of settling the Pigeons at a point in Nebraska for some days prior to release had resulted in the birds being confused. One also wonders whether the Pigeons used were in fact first-class homing material. In this connexion one small experiment quoted in the 1947 paper is of some interest. A pigeon-fancier in Nebraska sent ten birds for release in Pennsylvania, a reverse test. His birds were several years old and had flights of 200–400 miles to their credit. Three of these birds *homed across 1400 miles* to their Nebraska loft, and three others were recovered at points well to the *west* of Pennsylvania. The 'full discussion...in a later paper' of these results has not materialized.

Any idea of the use of the earth's magnetic field to obtain one or more navigational co-ordinates can be excluded. But this seems an appropriate point at which to consider briefly the reports that birds are affected by electrical disturbances, natural and artificial, since such effects are generally considered to have a bearing on the theory of magnetic navigation. There is a considerable conflict of evidence. Thauziés (1910) purported to show that thunderstorms produced poor homing results, but Gibault (1928) gave another analysis showing no correlation between natural electro-magnetic disturbances and the speed of homing. Such storms, of course, may have a direct effect on flying conditions. Yeagley (1951) claimed a general decline in the speed of pigeon-race winners with increasing sunspot activity of the day *before* the race, but made no check on other possible factors operating during the races, such as wind direction and force.

Casamajor (1927), Brown (1939), Anon. (1945), Yeagley (1947) report interference with orientation by non-pulsed wireless waves of various frequencies. But Gibault (1928), Casamajor (1930) and Meyer (1938) denied any such effect, while Kramer (1951 *b*) in a series of careful training experiments was unable to obtain a reaction to short-wave emissions. Reaction to *pulsed* radio, or radar transmissions have been reported by Poor (1946), Yeagley (1947), Drost (1949), Hochbaum (in Yeagley, 1951) and Knoor (1954). Negative results have been obtained by Hardy (1951) and Matthews (1951 *b*). It seems likely that in certain undefined conditions, flying birds may give a reaction to radar transmissions vastly exceeding in power any natural phenomena of this type. Schwartzkopff (1950) suggests that this may be due to electrical stimulation because of the amplitude modulation, through rectification in the tissues. Certain radar equipment can be made to produce audible sensations in the human subject at suitable pulse-rate frequencies. Barlow, Kohn & Walsh (1947) report visual sensations from electro-magnetic stimulation. The gross effects of powerful radar transmissions have been used to cook chickens, and to kill insects (Frings, 1952). Therefore, even if definite evidence that radar transmissions affect birds is obtained, it will certainly be no indication of their type of navigational equipment. At the same time it is well to be chary of dismissing possible extensions of known 'senses'. Lissmann (1951) has demonstrated a remarkable form of *proximate* orientation in certain fish. These set up a weak electrical field around themselves and apparently detect their surroundings and prey by changes in impedance. Such fish will react to a moving magnet. And Griffin (1953) has shown that a form of echo-sounding is used by a bird nesting in dark caves.

Orgel & Smith (1954) subjected Pigeons to a magnetic field fluctuating from 0 to 5 gauss (25 times that of the earth) 120 times a second without obtaining any conditioning to a stimulus-shock sequence.

CHAPTER 8

Theories of Complete Navigation by means of a 'Grid' Derived from the Sun's Co-ordinates

IT is curious that although human navigators have for centuries been obtaining their position in unknown areas from the sun's co-ordinates, it is only in the last few years that the possibility of birds doing likewise has been considered. Ising (1945), seeking a second co-ordinate to form a 'grid' with his proposed Coriolis force isolines, postulated a determination of longitude displacement by measurement of time differences in sunrise or sunset. Wynne-Edwards (1949) making a similar suggestion as regards longitude also pointed out that the measurement of the interval *between* sunrise and sunset varies with latitude. But the orientation we have demonstrated does not require observations at any particular time of day, and certainly does not require the bird to remain at the same point throughout a complete day. Ising recognized the effect of latitude changes on sunrise/sunset times, and suggested that the noon position of the sun was the only suitable one in such circumstances. But having, as he thought, provided means of determining latitude, he did not point out that the altitude of the sun at its noon position also gives an indication of latitude. This was done independently by Varian (1948), Davis (1948) and Wilkinson (1949). The last named made the important, indeed essential, suggestion that 'actual observation of the sun at noon is not necessary, occasional glimpses would combine with a time sense to enable its course to be constructed'. However, none of these writers considered the use of the noon position in longitude determination. Matthews (1951 *a*, *b*) put forward a synthesis of these ideas as a working hypothesis of complete sun navigation. This may be restated as follows. The essential feature is the *sun-arc*. This is inclined at an angle from the horizontal which is constant for a given place and is a measure of the latitude of that place. Farther north the arc is inclined at a lesser angle, farther south at a greater, so that the highest point on the arc is, respectively, lower and higher than at home (Fig. 25). This highest point is due south of the observer in the northern hemisphere and so gives a reference point in space by which the 'grid' is related to the surroundings. It is also reached at local noon, and so gives a reference point in time. The speed at which the sun moves round its arc is, for practical purposes, constant, at 15° an hour. When it has reached a particular point on its arc at home, it will have advanced further to an observer in the east, and less far to one in the west, the differences in arc angle (the angle round the arc from the noon position) being directly proportional to the change in longitude.

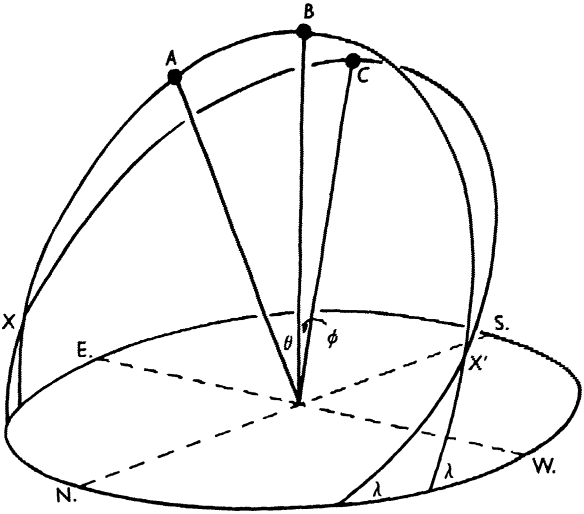

Fig. 25. Perspective diagram of the changes in sun arc consequent on a move to the south and west, at noon (home time). The altitude of the highest point of the arc (B) is greater (by ϕ) than at home (C). The inclination of the arc (λ) is also greater. The observed sun (A) has not moved so far round its arc (by θ) as it would have done at home. The bird is required to construct the 'foreign' arc by extrapolation of the observed movement of the sun at A, and to memorize the home arc. Note the crossing over of the arcs at two points, X, X'.

At home the bird will become familiar with the features of the sun-arc, and the sun's position on it at different (local) times.

These will be related to the internal 'chronometer' which is also an essential part of the hypothesis. In unfamiliar surroundings the bird will have to construct the sun-arc from observation. The suggestion is that it observes the sun's movement over a small part of its arc and extrapolates to obtain the highest point. Measurement of the altitude of this point, the angle from the horizontal, and comparison with the remembered value for home, say, the previous day, will give the latitude change. The arc angle from the observed sun to this highest point when compared with that obtaining at home for the same chronometer time will give the longitude change. An alternative means of latitude determination would be for the bird to extrapolate the arc back to its base, and to measure the inclination of the arc directly. This would only seem feasible in the summer half of the year, when the arc is far enough above the horizon for the lower part to pass over the east–west axis and so avoid parallax errors. An alternative means of longitude determination would be for the bird to project the sun's position downwards to the horizon and measure and compare the azimuth angles round from the south point. The highly variable nature of the azimuth angle with time of day, season and latitude, discussed in Chapter 5, makes its use much less likely than the stable arc angle, particularly as the latter would in effect be determined during the extrapolation process.

Before we examine this hypothesis in detail let us review the evidence that *some* form of complete sun navigation is used by birds. Matthews (1951*b*, 1953*a*, 1955*b*) has shown that the marked homeward orientation shown by Pigeons in critical releases (Fig. 12, p. 48) in sunny weather deteriorates markedly in conditions of heavy cloud (Fig. 26*a*, average deviation 73°) and breaks down completely with overcast skies (Fig. 26*b*, average deviation 86°). Kramer (1953*a*) has reported a similar disorientation in overcast conditions, though he only figures six bearings. Similarly Matthews (1952*a*) showed that the homeward orientation of Lesser Black-backed Gulls in sunny conditions (Fig. 49, p. 13) gave place to a disorientated scatter in heavily clouded and overcast conditions (Fig. 27, average deviation 4·7 points). The smaller number of Herring Gull bearings available for unfamiliar areas, thirty, also fail to give homeward orientation, average deviation 5·9 points, in cloudy conditions. It is interesting to recall Griffin's (1943) analysis of the bearings of twenty-five of his Herring Gulls. He found these

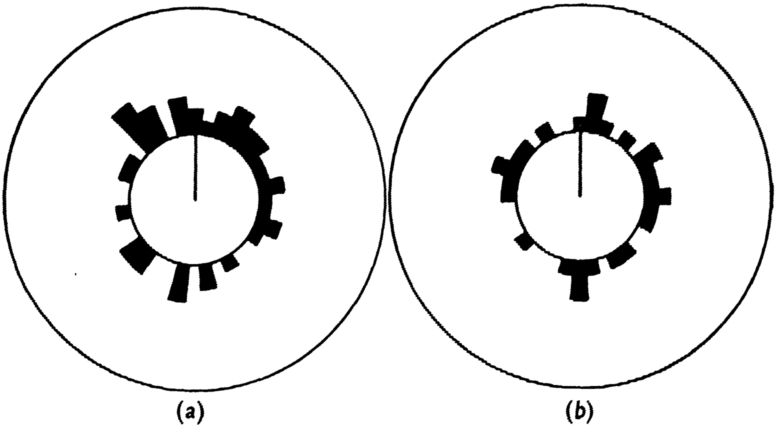

Fig. 26. Lack of orientation in Pigeons released at unknown points in novel directions in cloudy conditions. (*a*) With *c*. 8/10th heavy cloud. Two experiments from points 14 and 16 in Fig. 11, p. 47. (*b*) With complete overcast. Two experiments from points 14 and 17 in Fig. 11.

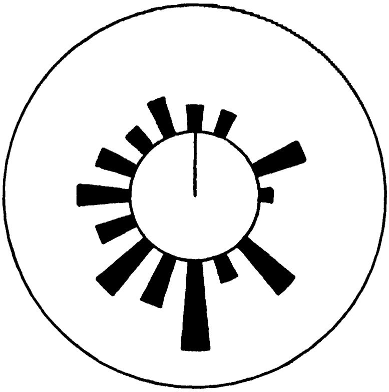

Fig. 27. Lack of orientation in Lesser Black-backed Gulls released at unknown points in cloudy conditions. Releases from 11 points.

to be random and used the result in support of random search hypotheses. But examination of his data shows that the relevant observations were made in cloudy conditions. Finally, Matthews (1953*d*, 1955*c*) found disorientation in cloudy conditions in the

Manx Shearwater. The 252 bearings shown in Fig. 28 have an average deviation of 3·9 points, and should be compared with Fig. 15, p. 51 which shows the strong homeward orientation in sunny conditions. With the Pigeons and Shearwaters it was possible to show, further, that the same individuals which gave good orientation in sunny conditions would scatter at random with overcast, and vice versa.

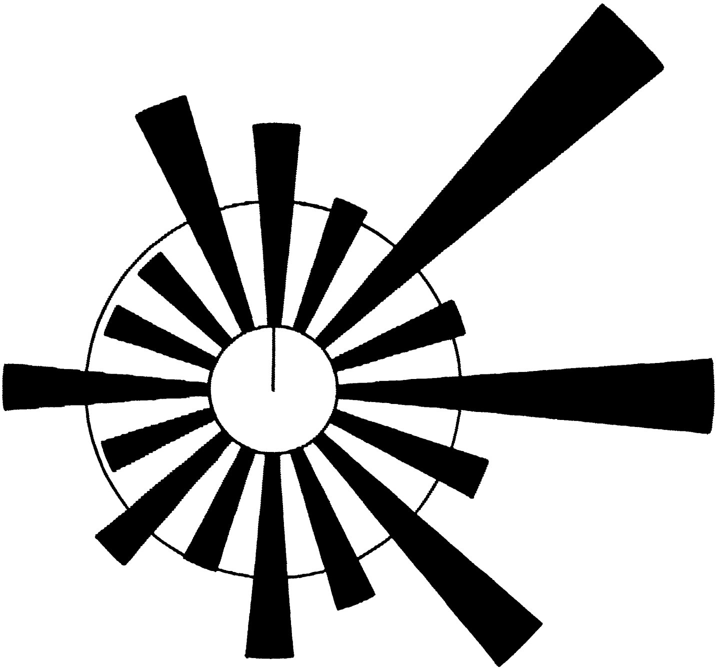

Fig. 28. Lack of orientation in Manx Shearwaters released at unknown points in cloudy conditions. Thirteen experiments from points 2, 3, 4, 5, 6, 8 and 10 in Fig. 14, p. 50.

The cloudy conditions at release might well not apply to other areas, and the cloud cover might break up where it had been present. A bird using sun navigation would stand some chance of seeing the sun and getting its bearings after, perhaps no very great delay. Also as we saw in Chapter 3, even random wandering is quite an efficient method of homing slowly from fairly short distances. So we must not expect the returns of birds released in sunny and cloudy conditions to show quite such marked differences as their orientations. Nevertheless there was a definite deterioration in the speed of return of pigeons released with overcast skies. Thus those in Fig. 26 gave only 43 % returns on the day, as against 71 % for equivalent sunny releases in Fig. 12. Shearwaters released from mid-May to mid-June in cloudy conditions failed to give the swift nearly complete returns obtained in sunny conditions (Table 8, p. 40). Only 128 of 171 returned (75 % as against 86 %) and considerably more slowly, as shown in Table 11.

Table 11. *Distribution of Shearwater returns, cloudy conditions early in season*

Nights after release	1st	2nd	3rd/4th	5th/10th	Later
Returns	6 %	32 %	28 %	16 %	18 %

The Shearwaters have been used to provide a further test of the essential part played by the sun in complete navigation. It is well known that Pigeons will not home at night, except after intense training over short distances, with additional guides such as lamps over the loft. Such results as have been obtained (Thauziés, 1913; Lincoln, 1927; Clarke, 1933; Nicol, 1945; Hardy, 1951) in attempts to extend their usefulness to military operations, are clearly explicable on a basis of developing an intimate knowledge of a local topography. But since Pigeons are such essentially diurnal animals this cannot be cited as evidence of a complete dependence on the sun for navigation. The Manx Shearwater, however, while habitually flying and feeding at sea during the day, only flies in the neighbourhood of the nesting area after dark—a habit probably enforced by their vulnerability on land to predator gulls. This does not imply any night navigation as the birds assemble in vast 'rafts' off the breeding islands well before dusk. But it does mean that they are willing to fly at night and so are available for an experiment to check whether they *can* show complete navigation at night. Twenty birds were released singly well inland, and thus in an unknown area, after dark (point 7, Fig. 14). They were only 60 miles, less than 2 hours' flying time, from home, giving them a generous margin to return there before the morning light *if* they were able to orientate themselves on release. But not a single bird got back that night. Eleven arrived the following night demonstrating that the urge to return was present, that only the ability to do so was lacking. This inference seems to be well justified although it could not be confirmed from behaviour at release as it was not possible to fit the birds with tail lights. Of six control birds released off the home island five were back in their burrows the same night.

This evidence, together with the disorientating effect of overcast skies on all four species investigated, strongly suggests dependence on a form of complete, bi-co-ordinate sun navigation. Two other tentative explanations have been advanced, however. Pratt (1953) suggested that overcast conditions might have a direct effect on the flight activity of birds, that they might cause an emotional upset which threw out some subtle means of orientation, such as the hypothetical parapsychological phenomena. Anyone familiar with the British climate will find it difficult to believe that our birds would be much disconcerted by cloudy weather. Matthews (1955*b*) has shown that when Pigeons are very familiar with a release point, after six previous releases there, overcast conditions have no effect at all on initial orientation. A subsequent release from another point showed that this result was not due to directional training, but to recognition of visual landmarks. The other suggestion, by Kramer (1953*a*) was that the birds derive their knowledge of the position of the release point by some entirely unknown means, but in terms of displacement in a particular compass direction. The bird then determines the latter with reference to the sun's position in azimuth. Without the sun, although it 'knows' that home is, say to the north-east, it has no means of telling where north-east is. Biologists will at once object to the implication of symbolic transference on the part of the bird. It will be remembered that the apparent symbolism employed by honey-bees in their dances has been shown by Vowles (1954) to be nothing more mysterious than a reaction at a given angle to one source of stimulus being transferred to another source when the first is excluded. Next, the suggestion throws us back to the unknown, as far as the primary means of navigation is concerned; not, be it noted, to the possibility of unknown 'senses' as such, but to an unknown 'sense' detecting and measuring *a completely unknown physical grid system.* Only thus would the information be in terms of a compass direction, requiring the use of a sun 'compass'. The unknown grid would further be peculiar in that it contained no intrinsic method of orientation with reference to the surroundings. We saw in the last chapter that both earth rotational and magnetic effects could theoretically serve as directional as well as positional systems. But these systems have been rejected on overwhelming grounds, and no others are known to the geo-physicists who have been taking an intimate interest in these problems during the last ten years. It would be a bold biologist who claimed that we know all the potentialities of living matter, but it is unthinkable that a complete geo-physical grid, prominent enough to be detected by birds and to be suitable for navigational purposes, should have escaped the notice of the physical scientists. Kramer (1954) claims that Pigeons' orientation is affected adversely by cold weather (– 1° to – 8° C.). It seems at least probable that this would be a result of changes in the landscape due to rivers freezing, snowfall, etc., especially as most of the releases were at short distances where landmarks are all important. Kramer's suggestion is basically implausible, but there are further, practical objections.

We have already discussed in Chapter 5 the difficulty of believing that birds using the sun as reference to move in one particular direction are taking their bearing from the sun's position in azimuth. This was because the latter was changing at a highly variable rate through the day, and also with the season. It was further altered by changes in latitude and longitude, which have particular cogency where long distance navigation is concerned. If, for example, the Shearwater released in Boston, U.S.A. (p. 28) had used its home (chronometer) time to determine from the sun's position in azimuth where east lay (having determined that east was the direction of home by means of the unknown grid) it would have flown north-north-west and would certainly not have been back in Wales 12 days later. Yet another objection is that, if the sun was being used only as a compass, overcast skies should not have such a drastic effect on orientation. The general position of the sun can be made out in all but the very heaviest overcast conditions, and we should therefore expect only a coarsening of the homeward orientation, not a complete breakdown. Releases on the training line are in fact less affected by overcast conditions, as shown in Fig. 29, average deviation 68°. The effect becomes progressively less as training in that direction proceeds, the deviation dropping to 62° for a first release at 80 miles, and to 43° for a repeat release at 80 miles—compared with 78° for a repeat release at a point *not* on a training line (Matthews, 1955*b*). It has also been shown for Pigeons (off training lines), gulls and shearwaters that cloud conditions which permit short glimpses of the sun itself (8/10th cover) were insufficient to allow of normal homeward orientation being established. A single glimpse should, in theory suffice to set the 'simple' sun-compass.

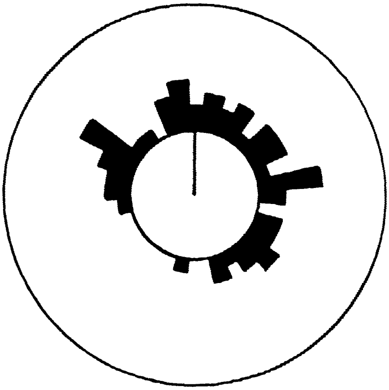

Fig. 29. Poor orientation in Pigeons released at unknown points in the training direction with overcast skies. Two experiments from points 7 and 9 in Fig. 11.

Lastly, if the sun-compass failed it should still be possible for the bird to find its way home over the unknown grid by a kinesis type of orientation behaviour (p. 79), 'feeling' its way along the resultant of the physical gradients. The birds would not really be disorientated though their initial departure on probing flights would appear random from the release point. Overcast conditions should then only slightly reduce the speed of return, particularly if the grid had a fine 'mesh' and so was interpretable over short distances. An experiment by Matthews (1955*b*) does not support this hypothesis. Twenty-five Pigeons of proven abilities in orientation and homing from distances up to 110 miles were released only 25 miles from home at a point visited twice before, at fairly long intervals. Heavy overcast conditions prevailed, the landmarks proved insufficiently known to assist orientation (cf. p. 56), and departure was essentially random. The day of release happened to be the first of a series of ten in which the whole of Britain was continuously wrapped in gloom. There was thus no opportunity for sun-navigation, but the unknown grid should have ensured the return of the birds on the following day at the latest. Instead, two birds were back on the day of release, two on the second day, six on the third, two on the fourth, one on the sixth, one on the eighth. These are the sort of results one would expect from random wandering. Six more birds arrived after the tenth day, when weather conditions improved, and five remained missing. There can be little doubt that the birds were *completely* disorientated, and not just lacking in a compass.

The remaining possibility, that birds are actually getting the co-ordinates of the release point, in relation to those of home, by information derived from the sun, was further investigated by Matthews (1953*a*, *c*; 1955*a*). An essential feature of the hypothesis (p. 93) is that the bird *compares* two sets of conditions of which it has had personal experience, those seen at home before transportation, and those seen at release. It is not required to have any 'nautical almanac' in its head to foretell future conditions. Now the only major change in the sun-arc through the seasons is its rising and sinking (Fig. 30). If the bird, having determined the highest point of the arc (necessary as both a spatial and temporal reference point) estimated its change in latitude from the altitude of that point, confusion might arise with changes in its altitude caused by the seasonal movement. This is relatively slow, varying from 10″ of arc per day at the solstices (22 June and 22 December) to 23′ of arc at the equinoxes (21 March and 23 September). Even at the latter no gross error would be introduced if the bird compared the noon altitude on one day with that on the preceding day without making allowance for the seasonal factor. If it were prevented from seeing the sun for a good many days at this critical period, distinctly misleading information would result. Such an experiment was carried out on two occasions shortly before the autumnal equinox. Pigeons which had been trained only from the west (to point 11, Fig. 11) were prevented from having any view of the sun, sky or direct sunlight for 6 and 9 days. Otherwise their conditions were kept as normal as possible, artificial light supplementing the diminished natural light. At the end of these periods of incarceration the sun's noon altitude was 2° 19′ and 3° 28′ lower than at the beginning. The pigeons were now

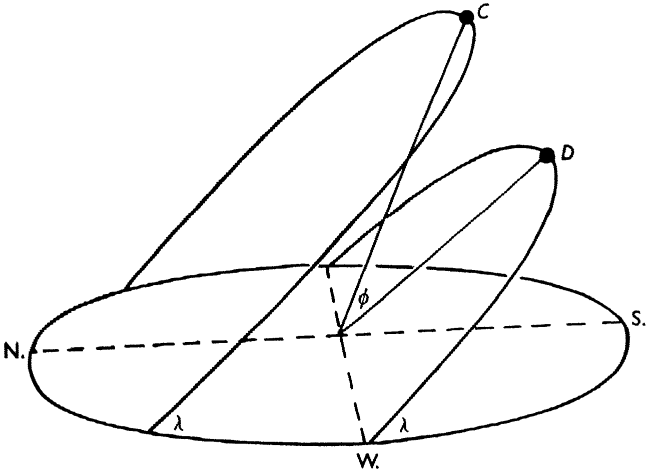

Fig. 30. Perspective diagram of the sun-arc at summer solstice and the equinoxes for latitude 51°. The highest point of the arc at *C* has a greater altitude than at *D* (by ϕ), but the inclination of the arc (λ) remains the same. Compare with Fig. 25.

taken to the south (to point 17, Fig. 11). The sun had a noon altitude 1° 04′ higher here than that at home, so the birds were confronted with a net fall in the sun's noon altitude of 1° 15′ and 2° 24′ since they had last seen it. This could be interpreted as due to a transportation to the *north* and the birds would then fly in a southerly direction. Fig. 31 shows that the majority of the birds did fulfil this prediction. Control birds incarcerated for the same period, but with full access to the sun and sky, orientated northwards in the true home direction. The results are statistically reliable, and allow of no explanation other than that of the hypothesis.

The case of the four experimental birds which started in the true home direction is interesting. They can be distinguished on statistical grounds from the main group, homed well and fast, and had good records in their previous flights. The general impression was that they were a better calibre of homers than the majority. It is possible that they had 'noticed' the daily sinking of the sun-arc prior to incarceration and allowed for it during the latter period. It seems more likely, however, that they were using the alternative method of latitude determination, estimating the inclination of the arc by extrapolation down to the sunrise/sunset position. The true difference between the home and release-point sun-arcs would be particularly apparent at the latter times, and this may account for the fact that, although only birds orientated in the home direction were back on the same day, returns from the falsely orientated birds had made up the leeway by the end of the next day.

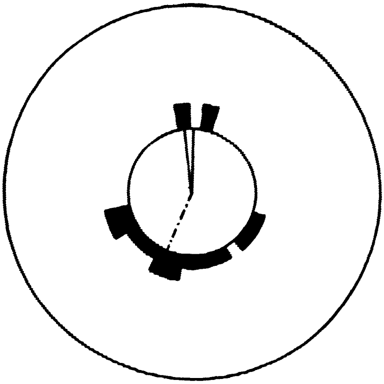

Fig. 31. False orientation in Pigeons released at an unknown point in a novel direction after a period of exclusion from sight of sun and sky. Two experiments from point 17 in Fig. 11. Coincided about the false, theoretical bearing (dot/dash line).

The sun's movement along its arc is constant (apart from certain minor aberrations) and so there are no seasonal changes in the arc angle to be exploited experimentally. The seasonal changes in azimuth angle have been discussed above (p. 99) and the lack of any westward tendency in the experimental birds shown in Fig. 31 is additional evidence that the azimuth angle is *not* used for longitude estimation or for obtaining a compass bearing. It would be interesting to confirm this by a release to the west after similar treatment. A more promising point of attack lay in the 'chronometers' of the birds. Whatever the physiological basis of such time-keepers it appeared probable that they would be kept in step by some external 'pacemaker' of which the light/dark rhythm appeared to be the most likely. Pigeons were therefore kept in a light-proof room and subjected for 6 days to a régime of light and dark periods of irregular length, combined with irregular feeding. On release to the west (their previous experience had been from the north) these birds gave a random scatter (average deviation, 100°) and slow returns. Controls, similarly imprisoned but allowed full view of sun and sky and fed regularly, orientated homewards and returned considerably faster than the experimentals. A similar test with Manx Shearwaters subjected to irregular lighting for 4 days, the dark periods being accompanied by a recording of the nocturnal cries of these birds, did not give conclusive orientation evidence owing to a strong wind at release. But there was a distinct lowering of homing success, only eight of sixteen experimentals returning as against fourteen out of sixteen controls. Other Shearwaters kept 4 days in constant light showed no impairment of homing ability. This agrees with other work on animal 'chronometers' in which it has been shown that rhythmical activities can continue for a considerable time in constant illumination. Indeed, Stein (1951) showed that trained responses, to anticipate food at a particular time, continued in such conditions after sleeping/waking rhythms had drifted out of phase or broken down completely.

To obtain critical proof of the part played by time-estimation in longitude determination, the obvious thing to do was to *alter* the 'chronometer' by a given amount so that the bird would derive false information from the sun-arc at release. A possible way of doing this would be to subject birds to an artificial day 3 hours in advance of normal and then release them east of home. *If* the chronometers had been advanced to coincide with the artificial day, the arc angle of the observed sun would be less than expected and this, on the hypothesis, would be due to transport to the *west*. The experimental birds should therefore fly eastwards in opposition to untreated control birds flying to the west. A second theoretical possibility would be for the birds to treat the changed 'day' to which they were subjected as being *due* to their having been transported far to the east. This would merely reinforce their tendency to fly west on release. To avoid this precautions were taken to persuade the birds that they were still at home, including in the case of the Shearwaters, the playing of a record of their nocturnal uproar, heard only at the breeding colony. *If* the only function of the sun was to act as an azimuth compass (p. 99) the treatment, if it succeeded in altering the chronometers, should result only in a displacement of the homeward orientation to the south; roughly speaking, south-west, but the precise direction depending on the time of day, season and latitude of release.

Four experiments were made with a total of ninety-nine Manx Shearwaters, half of them subjected to an advanced day for 4 days, the maximum time these birds could safely be kept incarcerated without weakening. Adverse weather conditions prevented any one test from being conclusive, but the overall conclusion was that the treatment did not disturb either orientation or homing. Pigeons subjected to similar treatment for 10 days again did not give any false orientation. If these Shearwaters and Pigeons had 'chronometers' which played a part in navigation they were less easy to manipulate than those of Hoffmann's two Starlings (p. 64). More drastic treatment was therefore embarked upon. Pigeons were first subjected to 4 or 5 days of the sequence of irregular light/dark periods and irregular feeding which had previously resulted in disorientation. *Then* with the chronometers, it was hoped, 'out of gear', they were subjected to the regular day 3 hours out of phase with the normal for from 5 to 19 days. Four experiments were carried out from east and (with the experimental day *retarded*) west and north of home (points 8, 5, 14, 2, Fig. 11, p. 47). Consistently throughout the series, which were all in good, sunny conditions, a significant majority of the experimental birds tended to leave the release point in the predicted false direction rather than the true home direction. Fig. 32 shows the results. The control birds orientated consistently in the home direction. The falsely orientated experimentals also returned significantly more slowly than the controls. Birds which orientated well as controls in one test, orientated falsely when used as experimentals in the next, and vice versa. As in the sun-altitude experiments, a minority of the experimental birds appeared to be unaffected by the treatment, and by their orientation and homing in these and other tests appeared to be superior to the general run of the Pigeons used. The implication is that their chronometers were much more stable. We have seen earlier (p. 52) that there is a wide range in individual navigational ability and it is reasonable to expect a variation in individual response to experimental treatment.

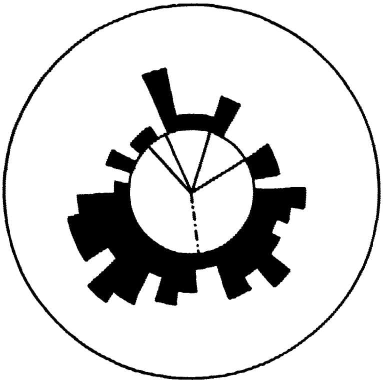

Fig. 32. False orientation in Pigeons released at unknown points in novel directions after treatment to disrupt and then reset their 'chronometers' to a false time. Four experiments from points 2, 5, 8 and 14 in Fig. 11. Coincided about the false, theoretical bearing.

The reorientation obtained in this series of experiments appears explicable only on the basis of longitude determination by the estimate of time (arc angle) differences. It is not consistent with the idea that the sun's only function is to act as an azimuth-compass. It might perhaps be added that longitude and time are one and the same thing, based on the regular rotation of the earth; there is no known, or indeed possible, method whereby longitude could be measured independently of time. The only way in which local time can be estimated is from the sun's position on its arc, local noon at the highest point. Taken together with the reorientation in latitude obtained in the altitude experiments, the evidence drives us to the acceptance of latitude/longitude determination based on the sun-arc. The only possible alternative would be the *instantaneous* measurement of the sun's altitude and azimuth at release and comparison with the values for the same chronometer time at home. This simply could not work as far as the azimuth measurement is concerned, for the bird would have no means of determining its reference point, north or south, from which the measurement was to be made. We have seen that any ideas of independent compasses based on magnetic or Coriolis forces are untenable (Chapter 7). The bird's eye has not the particular (pinhole) structure that might allow the sight of stars in the daylight, and the limited field of such a structure would in any case exclude the localization of the pole star with reference to the constellation patterns. A rapidly rotating gyrocompass is an anatomical impossibility.

The method could at the most give information on latitude displacement, and orientation from any direction could only be explained by postulating an unknown geo-physical gradient acting at a sharp angle to latitude, detected and measured by an equally unknown 'sense'. Further, even this instantaneous measurement of altitude would only be feasible at certain times of day. As Fig. 25 shows, the sun-arcs of different latitudes will run very close for much of their length and actually *cross* at two points in time in the early morning and late evening. The altitude measurement at these two times would be identical at both release point and home, and so could afford no information on latitude displacement. Even worse, perhaps, the sun's altitude at the more southerly place will actually be *lower* than that at home if measured before the cross-over point, *higher* if measured later. This cross-over point is above the horizon only in the summer, but it is then that most pigeon-racing and homing experiments take place. Kramer (1953*a*) confirmed the impossibility of latitude determination by this method. Nine groups of Pigeons, released at an unknown point 200 miles south of home at the precise cross-over time, orientated homewards, just as well as six similar groups released before or after that point. We must therefore return to the sun-arc hypothesis and examine its plausibility further.

Rawson & Rawson (1955) and Kramer (1955) report two experiments showing homeward orientation in pigeons prevented from seeing the equinoctial sun for 7–9 days, but allowed views of the sky and surroundings (cf. p. 102).

CHAPTER 9

Further Consideration of the Sun-Arc Hypothesis

A STRONG point in favour of the sun-arc hypothesis is its reliance on the one sense organ that we know to be exceptionally well developed in birds, the eye. Pumphrey (1948*a*) has given a lucid account of its potentialities which also emphasizes how little is known about them. There is no doubt, however, that the bird's eye is highly adapted to angular discrimination and for movement detection. The limits of the first are fairly certainly imposed by the basic structure of the retina, and Pumfrey put them at about 10″ of arc. The large aperture (pupil-diameter to focal-length ratio) needed to take advantage of the 'fine grain' retina is also found; it results from the flattened shape of the eye and from the fact that the pupil will remain fully open in bright sunlight. Further, Walls & Judd (1933) have suggested that the yellow oil droplets present in the cones have the function of suppressing the chromatic fringes which would hinder acute discrimination. Experience with the human eye confirms that the actual limits of resolution approximate to those suggested by retinal structure. Even with the very indirect training method, Grundlach (1933) found Pigeons resolving down to 23″ of arc at least. *If* the difference in the sun's noon altitude or, better, the inclination of the sun-arc, could be measured to 10″ of arc, a latitude displacement of only one-fifth of a mile could be detected; similar differences in arc angle represent a longitude displacement (in the latitudes of England) of just over a tenth of a mile. It is not suggested for a moment that a bird *could* navigate with such accuracy, but it is reassuring to find the accuracy obtainable by the method is between 250 and 500 times greater than that required for orientation at 50 miles, the nearest that orientation has been definitely demonstrated in the absence of known landmarks (p. 77).

Additional confidence in the possibility of a flying bird being able to measure small angles with great accuracy is given by the quite extraordinary stability of the bird's head in flapping flight. Despite the movement of the wings and body, the head, by virtue of an extremely fine compensating mechanism based on the semicircular canals, proceeds forwards with a rocklike constancy. There is ample proof of this in high speed cine-photographs, such as those taken by Brown (1953). A very beautiful example which will be familiar to many is that of a flying Flamingo in Disney's fine film, 'Water Birds'. This stable 'instrument bed' also enables us to credit the bird with the equivalent of an 'artificial horizon' or 'bubble sextant' which enables human air-navigators to measure vertical angles without reference to the visible horizon. The nature of the latter, hilly or flat, clear or misty therefore would not affect the issue. It may be mentioned in passing that the band-like *area* with pigmented borders, found in the eye of many birds such as shearwaters, bears a striking resemblance to the actual 'artificial horizon' in aircraft instruments. It is another satisfactory feature of the hypothesis that it brings in the well-developed sensory structure of the inner ear in an important secondary role. The many suggestions made about bird navigation led with persistency to this structure.

Although the acuity of the bird's eye is only about three times that of its human counterpart, there is, as Pumfrey says, 'abundant evidence that birds as a whole are immensely more successful than man at detecting movement. . . ' in circumstances where they '. . . often have to look up at a clear sky or down at uniform pasture and moor and sea'. There are at least three features of the bird's eye that probably enhance its powers of movement detection. First, nearly all the retinal surface lies in the image plane, so that all distant objects are sharply focused. There is also much less difference between the concentration of cones in the fovea and in the rest of the retina than there is in the human eye. The net result is that the bird has a sharp, detailed picture simultaneously of its whole visual field, and does not have to build up such a picture by scanning movements as we do; a bird does not have to focus an object to be aware of its shape and movement. Secondly, Pumphrey (1948*b*) has suggested that the characteristic steep profile of the central fovea can, by imposing a momentary distortion, enhance the appearance of movement, and contribute to a 'phenomenal ability to detect angular movement'. Thirdly, Menner (1938) suggested that the *pecten*, primarily a nutritive organ, plays a vital part in the dioptric system by virtue of the foliated shadow it casts on part of the retina. He concluded that it enhanced the ability for movement detection. This was based on the use of models of the apparatus and by showing that the foliations were particularly well developed in those species dependent on the capture of moving prey. Crozier & Wolf (1943*a*, *b*), using a refined flicker-fusion technique, fully confirmed Menner's postulates. The exact reason for the phenomenon is not understood, but the shadows probably increase the contrast as the observed object moves across the field.

It must be emphasized that no quantitative data are available as to the effectiveness of these devices in enabling the detection and evaluation of movement, in particular the sun's movement along its arc. We can, however, fall back to the basic limits provided by the structure of the retina and assume, for the sake of argument, that, as with acuity, the dioptric system is so developed as to take full advantage of that structure. The sun moves through the minimum arc of 10″ of arc in ⅔ second of time. Since at least three points are required to determine the curvature of an arc, the minimal time interval of observation would be 1⅓ seconds. Again it is not claimed that a bird *can* make such a swift estimate, but this is the basic figure for consideration.

The characteristic behaviour of homing birds at release is to dally in the area for a noticeable period, either circling or making more random evolutions, before they depart on their final line. Such behaviour has been commented on again and again by different observers with various species of wild birds and with Pigeons. The subjective impression gained was that, during this initial period of undirected flight the birds were 'getting their bearings', and that some finite time was required for them to do so. The objective measure of this initial period has been the interval between release and the time at which the bird was lost from sight in binoculars. There is clear evidence that this 'orientation time', 'vanishing time' or 'time in sight' as it has been variously termed, contains a factor concerned with orientation. This is the relation that its average value has with the presence or absence of good orientation. Table 12 lists eleven experiments with Pigeons (Matthews, 1953*a*, 1955*b*) in which very poor orientation or random scatter was obtained, either by release with overcast skies or by release in the marginal zone around 25 miles where the navigational aid appears not to function (p. 78). The average time in sight for these disorientated releases is compared with the average time in sight of the *same* birds at preceding well-orientated releases. It will be seen that in every case the latter value is much lower.

Table 12. *The relation between 'time in sight' and presence or absence of orientation*

	Cloudy conditions							Marginal releases				
o. of birds	13	16	17	42	18	27	20	20	12	20	12	217
v. deviation	78°	93°	70°	78°	62°	73°	78°	84°	88°	62°	70°	76°
v. time (min.)	7·8	7·1	5·7	4·2	5·6	4·5	5·1	5·0	5·1	4·7	4·9	5·1
revious av. .ime (min.)	4·9	4·5	4·9	3·0	3·4	2·9	3·6	3·6	3·8	3·6	3·8	3·6

But factors other than orientation are undoubtedly concerned in the total 'time in sight'. With Pigeons, the desire to fly in company is strong but can be diminished by repeated single releases. Matthews (1953*b*) showed that untrained birds and those with little experience of single flights had a high value, 5·6 to 5·8 minutes, even in good weather conditions. With but little more experience the value dropped sharply and thereafter fluctuated irregularly between 3·2 and 4·4 minutes, showing no further consistent reduction. The overall figure for the 652 releases in Table 13 was 4·1 minutes. A further reduction can be made by releasing the birds in small groups (Matthews, 1951*b*; Kramer, 1953*a*), but this method robs the results of statistical significance unless very large numbers of birds can be used. The evidence also suggests that such grouped releases give less scatter than single bird releases. This may be due to the best navigator in each group setting the direction, or to some form of unconcious co-operation with the errors of the individual determinations cancelling out. This would lead to greater accuracy in less time.

Table 13. *Variation in the 'time in sight' and the associated accuracy of orientation*

	Time in sight (minutes)							
	< 2	-2½	-3	-3½	-4½	-5½	Over	Total
Repeat releases								
No.	4	13	22	14	14	5	28	100
Av. deviation	38°	29°	33°	30°	32°	52°	68°	43°
Training releases								
No.	15	33	29	27	33	21	54	212
Av. deviation	24°	33°	65°	57°	44°	32°	45°	44°
Critical releases								
No.	42	54	75	45	46	30	47	340
Av. deviation	57°	37°	43°	59°	48°	38°	52°	47°
All releases								
No.	61	100	126	86	93	56	129	652
Av. deviation	47°	34°	47°	54°	44°	37°	53°	46°
Percentage of total	9	15	20	13	14	9	20	100

Pratt (1955) suggested that much of the time in sight was spent in circling to gain height, and found a difference between Pigeons released at the foot and at the top of a 100-foot tower. In one instance the difference averaged 1 minute, in the other, 2½ minutes. It certainly does not take a Pigeon a minute, let alone two and a half, to gain a mere 100 feet in height. Moreover, although untrained birds such as Pratt used do tend to fly rather high, the experienced Pigeons, and Shearwaters too, normally fly in the 100- to 200-foot zone, and down to 20 feet or less in a strong head wind. It is certain that the majority of birds circling near the release point are *not* continuing to gain height once the operational level has been reached. Matthews (1955*a*) also found a lower average time in sight for tower releases, simply because the birds tended to fly below the level of the observer (180 feet) and were more easily lost against the landscape background than against the open sky. For this reason he found releases in flat open country from ground-level to be much more satisfactory.

The time taken to reach the limit of visibility will of course be included in the 'time in sight'. This limit depends on a number of factors, eyesight and experience of the observer, optical aid used, background, clarity of atmosphere, direction of sunlight, colour of bird and its attitude to the observer—tail on or broadside on. But when viewing conditions are favourable an experienced observer using 16 × 40 binoculars is unlikely to follow a Pigeon flying directly away from him for more than 1 minute. If we subtract this from the total time in sight we have a measure of the extra time spent near the release point. In Table 13 are given the results of 652 observations made on Pigeons released in sunny conditions at distances of 50–130 miles (Matthews, 1951*b*, 1953*a*, 1955*a*, *b*), not including any untrained birds. It will be seen that very few of the birds (under a tenth), spent less than a minute longer than was 'necessary' near the release point. Only a quarter dallied for less than 1½ minutes.

It will further be seen from Table 13 that the birds lost quickly were quite well orientated, and that the accuracy of orientation did not increase steadily the longer the bird remained in sight. It follows that the birds dallying for an excessively long time were doing so for reasons unconnected with the orientation process. This does not necessarily mean that orientation would not have been improved by a longer period of observation if these extraneous factors were removed. Indeed, in Kramer's (1953*a*) experiment, Pigeons which were exposed at the release point for 1 or 2 days, before liberation in groups, gave a better orientation (average deviation 26° as against 46°) than those released after only half a minute's exposure. Unfortunately, only five and ten groups respectively were concerned, insufficient for statistical assessment. Nor is it permissible to conclude that the birds quickly lost to sight were necessarily orientated by the end of the 'excess' period of time. A competent release technique should ensure that birds are liberated in all directions, and so we should expect a quarter to start out, by chance, within 45° of the home direction. The orientation process could be taking place while the bird maintained this chance trend, yet the appearance would be of orientation from the moment of release. Apart from the liberation technique the immediate direction of flight on release is particularly liable to bias by extraneous factors which play little part in the bearing of the final vanishing point, such as moderate winds. If the birds have an innate or learned directional bias, they may start out in that direction and, if it is still appropriate, will be swiftly lost on a good bearing. If it is no longer appropriate such behaviour may be a disadvantage—compare the orientation under 2 minutes in Table 13 for training and critical releases.

To reach a conclusive decision on the question of the minimum interval after release in which orientation can occur, two approaches are open. Either it must be shown that a number of individual birds consistently make swift, well-orientated departures, or the orientation of a large number of birds must be shown to be just as good after the minimum interval as when they are finally lost from sight. Following the first method, the histories of 122 individual Pigeons were examined. They all had at least three sunny releases at a distance to their credit, and accounted for 549 of the sorties shown in Table 13. Of these birds 57 % had records of at least one disappearance within 2½ minutes of release, but *not one* had a consistent record of such swift starts. Only ten had consistent records of starts within 3 minutes, i.e. of 1½–2 minutes of excess time in sight. This does not favour suggestions of nearly immediate orientation.

The second approach is being exploited. Kramer (1953*a*) claimed that his grouped releases were orientated within 40 seconds of their being exposed to the sun, including only 10 seconds in flight. This, however, was a purely subjective estimate, and it is certainly rash to try and decide when a flying Pigeon has made up its mind. Recently the parapsychologists Pratt & Thouless (1955) claim to have found 'strong indications that birds are capable of choosing the direction toward home within 10 seconds after they see the sun'. They made some attempt at objectivity by recording the bearing at 10, 20 and 40 seconds after release, together with the final bearing. One observer would be responsible for two bearings, keeping the first in mind, related to some land mark, until the second was noted. This clearly leaves a lot of room for fallibility of memory. Most of the Pigeons were exposed in openwork crates at the release point for up to several hours but with an opaque object (angle subtended unspecified) between them and the sun. Others were treated similarly but the sun allowed to shine on the crate. The final bearings at which the birds were lost from sight (no times given) do show a rather poor though significant homeward trend, seventy-four birds with an average deviation of 56°. But the sixty-four bearings given at 10 seconds from release have an average deviation of 84°, a random scatter, as will be seen from Fig. 33. No significant improvement in orientation was obtained by 20 seconds or by 40 seconds (60 seconds in the case of eight birds) when the average deviations were 78° and 76°, neither differing significantly from random. One must draw a conclusion rather different from that of the authors: their results completely fail to show any immediate homeward orientation. A more objective technique is in use by the present writer in which a plumb-line suspended from the observer's binoculars moves round a degree circle, its position at specified intervals being marked by an assistant using numbered pins. Work is still in progress at the time of writing, but the present trend of results is against any immediate or swift orientation.

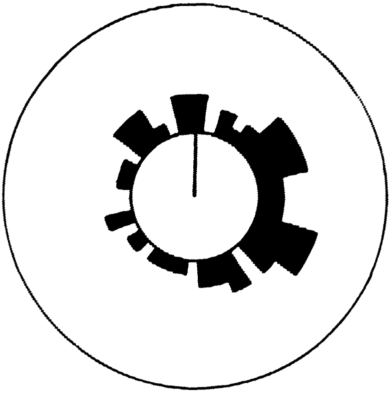

Fig. 33. Lack of orientation in Pigeons 10 seconds after release at an unknown point in sunny conditions. (Constructed from data in Pratt & Thouless, 1955.)

The techniques of prior exposure used by Kramer and Pratt & Thouless were designed to ensure that the birds were light-adapted at release, the implication being that part of the time in sight was normally utilized for this purpose; Matthews kept his birds in indirect natural light or, in a low intensity of artificial illumination before release. But exclusively diurnal birds like Pigeons show a negligible degree of dark adaptation and are thus nearly blind at night. Conversely their eyes will be fully operational directly they are exposed to high illumination, as is indeed obvious from their behaviour in such circumstances. Pumfrey has emphasized a salient point, to be borne in mind when one is tempted to interpret the reaction of a bird's eye as if it were our own—the bird's eye has the great advantage of continuous selection as a daylight receptor, whereas we have a poor re-modelling of a nocturnal type of eye.

Provided that a portion of the sun-arc can be observed and evaluated, the requirement that the bird should extrapolate to the highest point of the arc does not present much difficulty. Extrapolation of the path of moving objects is essential in birds feeding on moving prey, such as a plunging Gannet. Conversely birds flying fast in close proximity to objects must be able to judge their own track with accuracy. The 'good eye' of an expert player in ball games or of the crack shot depends upon an ability for extrapolation. In the case of the sun, too, the problem is much simplified by the fact that it is an object moving at a constant speed and in a relatively limited number of ways and without any complications of parallax. There is some evidence among the Pigeon data that extrapolation is indeed occurring. The 552 first time releases in Table 13 were spread from 05.00 to 15.00 hours G.M.T. It is found that the proportion of gross errors (more than 90°) was higher for those birds released early in the day, up to 09.00 hours, than for those released within 3 hours of noon, respectively 19 % of 232 and 11 % of 320. The difference, though small, is quite significant ($P = 0{\cdot}02$) on this scale. Greater errors would, of course, be expected when more extrapolation to the highest point was required. Excluding these gross errors and considering the releases to the north and south of the loft, we find a curiously low proportion of well-orientated sorties (error less than 22·5°)

within an hour of noon, 25 % of 69, as against 42 % of 251 at other times of day. For releases to the east and west the difference is negligible (2 %) instead of being significant ($P = 0{\cdot}02$). Small errors in extrapolation near the noon position would concern arc angle (i.e. longitude estimation), and *small* errors in longitude estimation would be apparent when the main displacement was in latitude rather than in longitude. The disorientating effect of heavy though broken cloud might be due to its movement in close proximity to the sun, causing confusion in the estimation of the latter's movement.

We have already seen that the sun-arc provides a fixed reference point (its highest point always being due south), and that this may well be used when estimating a fixed direction, innate or learned, or when maintaining a given bearing. The bird could also use the south point to 'set its map' with reference to the surroundings, and so depart in the home direction without testing the gradients of its navigational grid. Although reaction to changes in the sun-arc on these terms does not involve any symbolic transference from one sense to another (p. 98), it still has an element of symbolism about it. Thus the bird would have to 'know' that when the noon altitude (or inclination) of the arc was less than at home it must fly south, when greater, north; when the arc angle is smaller it must fly east, when greater, west. It would be logically more acceptable if the bird reacted to a changed stimulus by a movement to restore the norm. An advantage of the sun-arc hypothesis is that it can be stated in just such terms. If the arc is too low in the sky, the bird seeks to correct this by flying towards the arc; if it is too high, away from the arc. If the sun has not moved far enough round its arc the bird seeks to correct this by flying in that direction which adds its movement to that of the sun; if the sun has moved too far, in that direction which subtracts its movement from that of the sun.

We may consider the effect of a trans-equatorial release of birds from a northern home (say, 51° N.) in these terms. If the release is south of the co-latitude (51° S.) homeward orientation should still be observed. The arc inclination would be less than at home, the bird, flying towards the arc, would move northwards. If the release is north of the co-latitude but below the equator, the inclination of the arc would be more than at home, the bird flying away from the arc would move falsely southwards. But the southern hemisphere experiences the opposite season to the northern, so that, for instance, the noon altitude at the co-latitudes is the same only at the equinoxes. To be critical, therefore, the release would have to be at a latitude and at a season such that both the noon altitude and the arc inclination were greater than in the bird's northern home. This could be most readily achieved in the northern winter, since a point well south of the equator would be preferable. Near the equator confusion might arise from the sun-arc being near vertical, and though a demonstration of such confusion would be useful, it would be less convincing than a completely false orientation. Swift transport by air would be necessary since the birds would have to be kept in close confinement and prevented from observing the transitional changes in the sun-arc. Otherwise the birds would be in a similar position to migrants crossing the equator by their own efforts. These may either be regarded as continuing to fly in one direction through the sun-arc, or as changing their orientation with reference to that arc after a transitional period. Such changes in 'standard direction', quite apart from the effects of 'leading-lines', have been clearly demonstrated during migrations in the northern hemisphere.

The work of Kramer, Hoffmann and Matthews discussed earlier has established beyond doubt the existence of some form of chronometer mechanism in birds. The function of the day/night alternation as a pace-maker is clear, but the nature of the basic rhythmic processes which can keep the chronometers running for many days when the external rhythm is removed remains quite obscure. We need information on the nature and accuracy of these chronometers independently of their function in orientation. Stein's (1951) work with passerines, while affording valuable confirmation of the existence of such chronometers, was not sufficiently precise for our purposes. Accurate time-keeping mechanisms have been demonstrated in many arthropods and these might be used to give information by analogy. Even humans have produced remarkable performances; MacLeod & Roff (1936) found that two subjects shut in sound-proof rooms for 48 and 86 hours, estimated the time with such accuracy that their cumulative errors amounted to only 0·9 and 0·8 %.

The remaining feature of the hypothesis to be considered is the requirement for the bird to have an accurate memory of the sun-arc characteristics at home. Here again we have no direct independent evidence, but the results of training experiments (p. 56) have shown that once a problem involving visual stimuli has been learned the degree of retention is very high over several years. Such learning and retention would be at their best where the 'problem' was a natural one, of intrinsic importance in the normal life of the bird. In most homing experiments the retention is required no more than for a few days, in migration for 6 or 8 months. It may be noted that the seasonal changes in the sun-arc do not affect the issue since the rise or fall of the arc will be in the same sense as the direction of migration on both spring and autumn migrations. In many cases (Corti, 1931; Geyr von Schweppenburg, 1943) the departure and return dates are equidistant from the summer solstice and the daily *rate* of change will also be the same. It is interesting to note that it is often the long distance migrants that are precise in their arrival and departure. The Great Shearwater with its remarkable navigational problem (p. 2) departs, according to Rowan (1952), in the second week of April from its isolated breeding-grounds and returns at the beginning of September, dates 10 weeks on either side of the summer solstice. The return is much earlier than would seem 'necessary' since eggs are not laid till November. In species where this does not apply, e.g. departure in September/October and return in April/May, the difference in rates of rise or fall of the arc will still be slight and such as to cause an overshoot, i.e. would take the birds through the required areas, which could be recognized visually. Also these cases concern migrants with relatively restricted homes connected in the first instance by flight in one 'standard' direction. This direction will be reinforced by experience, coupled with a more precise estimate of the distance to be covered. The main function of the homing ability would then be to correct any involuntary displacements from that track such as may be produced normally by strong beam winds, or abnormally by the experimenter. The correction could either be in terms of a return to the point where displacement occurred, or by a vector change in the migration direction. The data in Fig. 4, p. 14 would suggest the latter.

While we are touching on migrations, we may recall that the primary stimuli for the onset of migration appear to be changes in day-length, which are governed by the rising and sinking of the sun-arc. Again, one of the main purposes of migration appears to be to take advantage of the longer days in higher latitudes, which allow more food to be collected for the young. The length of day is correlated with the inclination of the sun arc. Thus it seems possible that the sun-arc may provide the purpose, cause and guide of migration.

And that is as far as we can go on the present evidence. Work is proceeding actively in several centres and no doubt this attempted summary of the present position will soon be out of date. The reality of navigational ability in birds is an established fact. No theory of the physical basis of bird navigation remains in the field except that involving the sun. This the evidence strongly supports, and the only type of sun navigation that fits the observed facts and is satisfactory from the logical point of view is that proposed by the sun-arc hypothesis. Even if future work proves this particular hypothesis faulty, it seems fairly certain that the final solution will have to be a reinterpretation of the way in which the sun's position in the sky can serve to give the bird its position relative to home. It also seems probable that field experiments of the type we have been describing have reached their useful end, except, perhaps for trans-equatorial tests. For further progress the problem will have to be brought into the laboratory. In countries blessed with sunny climates much may be done with some form of coelostat, in our own cloudy island a mechanical sun simulator, faithfully reproducing the appearance and movement of the real sun, would seem to be a prime requirement.

SCIENTIFIC NAMES OF SPECIES MENTIONED

Albatross, Wandering. *Diomedea exulans.*

Blackbird. *Turdus merula.*
Blackbird, Redwinged. *Agelaius phoeniceus.*
Blackcap. *Sylvia atricapilla.*
Bluethroat. *Cyanosylvia svecica.*
Buzzard. *Buteo buteo.*

Chaffinch. *Fringilla coelebs.*
Chickadee. *Parus atricapillus.*
Chough, Alpine. *Coracia graculus.*
Coot. *Fulica atra.*
Cormorant. *Phalacrocorax carbo.*
Cowbird. *Molothrus ater.*
Crow, Hooded. *Corvus cornix.*
Crow, Prairie. *Corvus brachyrhynchos.*
Cuckoo, Bronze. *Chalcites lucidus.*
Curlew, Bristle-thighed. *Numenius tahitiensis.*

Duck, Wood. *Aix sponsa.*

Falcon, Peregrine. *Falco peregrinus.*
Finch, House. *Carpodacus mexicanus.*
Frigate Bird. *Fregeta magnificens.*

Gannet. *Sula bassana.*
Goldfinch. *Carduelis carduelis.*
Goose, Canada. *Branta canadensis.*
Goshawk. *Accipter gentilis.*
Greenfinch. *Chloris chloris.*
Gull, Black-headed. *Larus ridibundus.*
Gull, Common. *Larus canus.*
Gull, Great Black-backed. *Larus marinus.*
Gull, Herring. *Larus argentatus.*
Gull, Lesser Black-backed. *Larus fuscus.*

Hawk, Sparrow. *Accipter nisus.*

Jay, California. *Aphelocoma californica.*
Junco, Sierra. *Junco oreganus.*

Kestrel. *Falco sparverius.*

Mallard. *Anas platyrhynchos.*
Man-of-war Bird. *Fregeta magnificens.*
Martin, House. *Delichon urbica.*
Martin, Sand. *Riparia riparia.*
Moorhen. *Gallinula chloropus.*

Nuthatch. *Sitta europaea.*

Oriole, Baltimore. *Icterus galbula.*
Ousel, Ring. *Turdus torquatus.*
Owl, Cape Barn. *Strix flammea.*

Petrel, Leach's. *Oceanodroma leucorrhoa.*
Petrel, Storm. *Hydrobates pelagicus.*
Pigeon, Homing. *Columba livia.*
Pigeon, Rock. *Columba livia.*
Pintail. *Anas acuta.*
Plover, Golden. *Charadrius dominicus.*
Plover, Semi-palmated. *Charadrius semipalmatus.*
Puffin. *Fratercula arctica.*

Quail, Valley. *Lophortyx californica.*

Raven. *Corvus corax.*
Redstart. *Phoenicurus phoenicurus.*
Redstart, Black. *Phoenicurus ochruros.*
Robin. *Erithacus rubelcula.*
Robin, American. *Turdus migratorius.*
Rook. *Corvus frugilegus.*

Shearwater, Great. *Procellaria gravis.*
Shearwater, Manx. *Procellaria puffinus.*
Shelduck. *Tadorna tadorna.*
Shrike, Red-backed. *Lanius collurio.*
Siskin. *Carduelis spinus.*
Skua, Great. *Catharacta skua.*
Skylark. *Alauda arvensis.*
Sparrow, Fox. *Passerella iliaca.*
Sparrow, Gambel. *Zonotrichia leucophrys.*
Sparrow, Golden-crowned. *Zonotrichia coronata.*
Sparrow, Hedge. *Prunella modularis.*
Sparrow, House. *Passer domesticus.*
Sparrow, Song. *Melospiza melodia.*
Sparrow, Tree. *Passer montanus.*
Starling. *Sturnus vulgaris.*
Stork, White. *Ciconia ciconia.*

Swallow. *Hirundo rustica.*
Swallow, Rough-winged. *Stelgidopteryx ruficollis.*
Swan, Mute. *Cygnus olor.*
Swift. *Apus apus.*
Swift, Alpine. *Apus melba.*

Teal. *Anas crecca.*
Tern, Arctic. *Sterna macrura.*
Tern, Common. *Sterna hirundo.*
Tern, Noddy. *Anous stolidus.*
Tern, Sooty. *Sterna fuscata.*
Thrasher, California. *Toxostoma redivivum.*
Tit, Blue. *Parus caeruleus.*
Tit, Great. *Parus major.*
Tit, Long-tailed. *Aegithalos caudatus.*
Tit, Pallid Wren. *Chamaea fasciata.*
Towhee, Anthony. *Pipilo crissalis.*
Towhee, San Diego. *Pipilo maculatus.*

Warbler, Barred. *Sylvia nisoria.*
Whitethroat. *Sylvia communis.*
Woodpecker, Middle Spotted. *Dendrocopus media.*
Wren, House. *Troglodytes aedon.*
Wryneck. *Jynx torquilla.*

Yellow Hammer. *Emberiza citrinella.*

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This list of references aims at being comprehensive but not exhaustive. It is hoped that it includes every account of experimental work on bird navigation, and every paper setting out an original theoretical contribution. Preliminary announcements, summaries and translations are excluded in favour of the main publication concerned. Papers which are reiterations of previous publications are represented only by the most comprehensive of the series. No attempt has been made to include every commentary on the subject, which are legion, but only those that were both comprehensive and authoritative at the time when they were written, viz. Claparede (1903), Watson & Lashley (1915), Rabaud (1928), Schüz (1931, 1951, 1952), Alexander (1934), Bierens de Haan (1934), Koehler (1943), Griffin (1944, 1952*c*), Gray (1946), Kramer (1948), Matthews (1948, 1951*a*, 1953*c*), Odum (1948), Verwey (1949, 1954) and the more general surveys of Thomson (1926, 1936), Wachs (1926) and Drost (1951). To these the compilation of this monograph owes much. A few guiding references have been given to work in allied fields but outside the limited scope of this monograph.

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